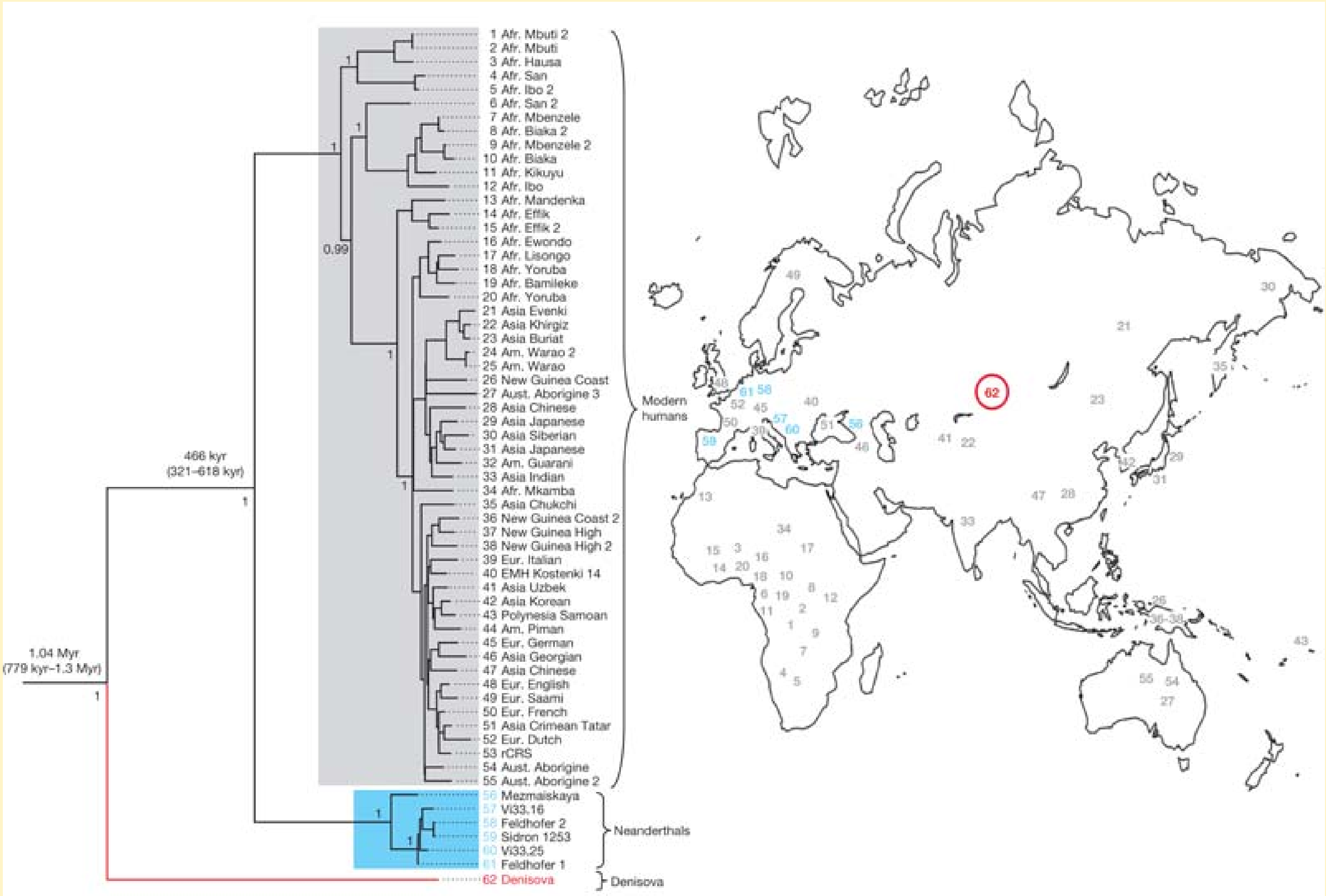
BIOL 432 - Evolution

Lecture 9



J Krause *et al.* *Nature* **000**, 1-4 (2010) doi:10.1038/nature08976

Selection

- http://www.youtube.com/watch?v=a38KmJ0Amhc&feature=PlayList&p=61E033F110013706&index=0&playnext=1
  - Start at 5:21 min

Onychophoran
(velvet worm)

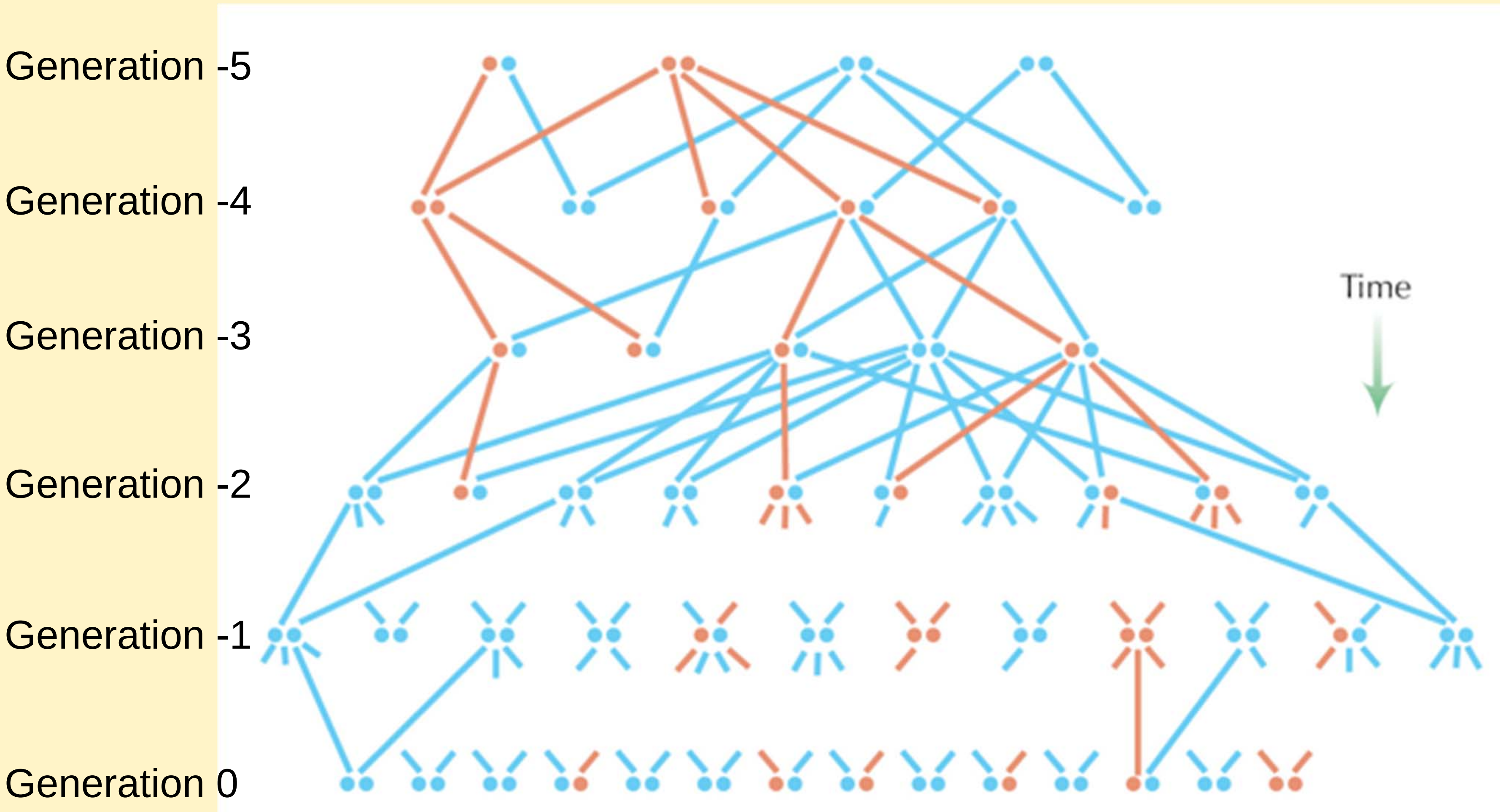
Fitness

- Definition: “The number of offspring an individual leaves after one generation”
  - Simple definition, but difficult to measure

Fitness at the molecular level

- *Gene*: “The number of copies that a particular gene leaves after one generation”
- *Allele*: “Average fitness of genes carrying the particular allele”
- *Genotype*: ”Average fitness of individuals carrying that genotype”

Fitness is not only associated with natural selection



- Drift is caused by random, non-inherited variation in fitness between individuals

Components of fitness

- Overall fitness can be deconstructed into different components
- E.g.:
  - Surviving to adulthood
  - Chance of finding a mate
  - The number of offspring for each couple

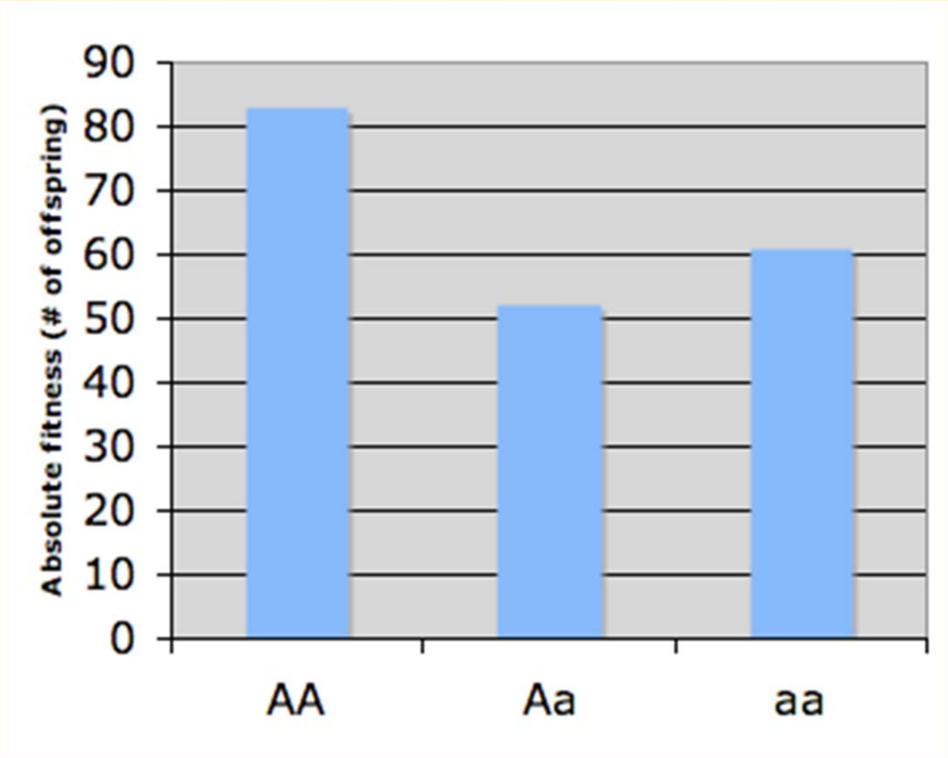
W: Fitness when generations are discrete

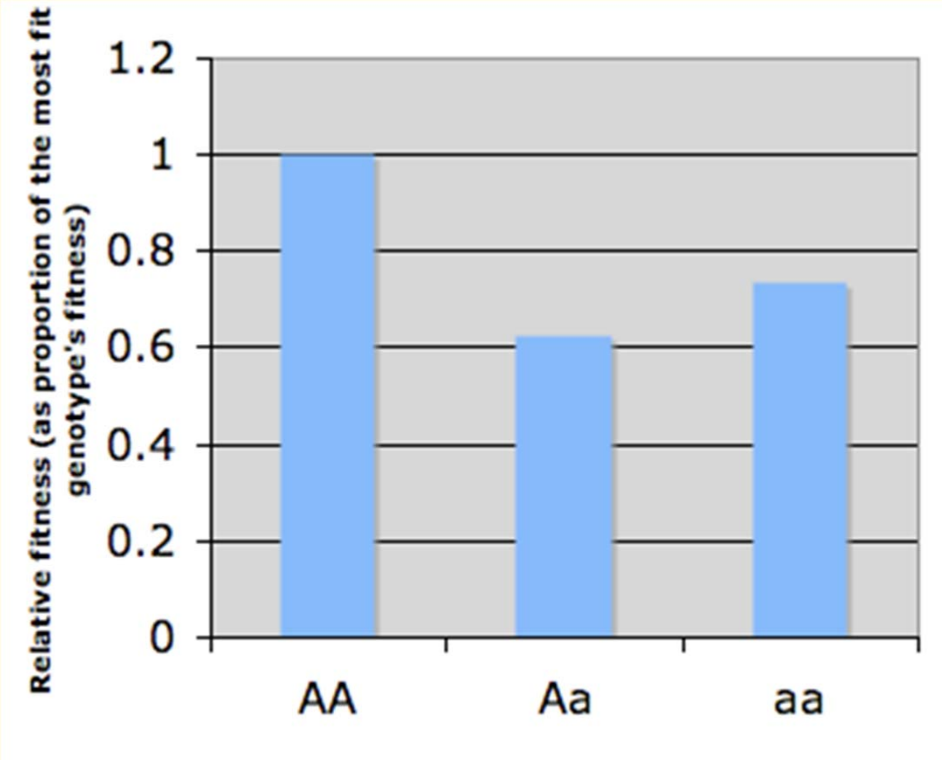
- W for a specific genotype:
  - -Fitness components are multiplied

W = average number of offspring after one generation = average probability of survival to adulthood * average probability of finding a mate * average number of offspring per adult

How big should W be to maintain a constant population size in a bisexual population?

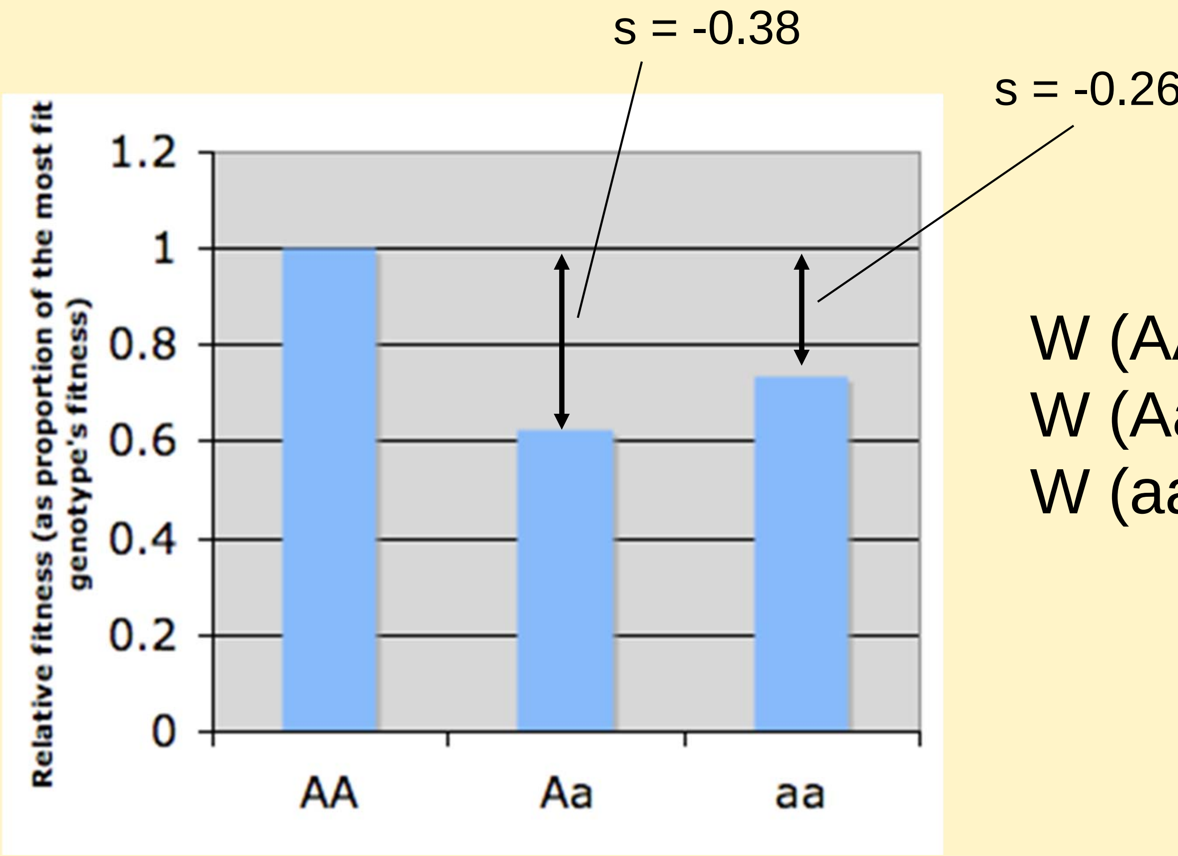
Absolute vs. relative fitness





- Why does this distinction represent the separation of ecology from evolution?

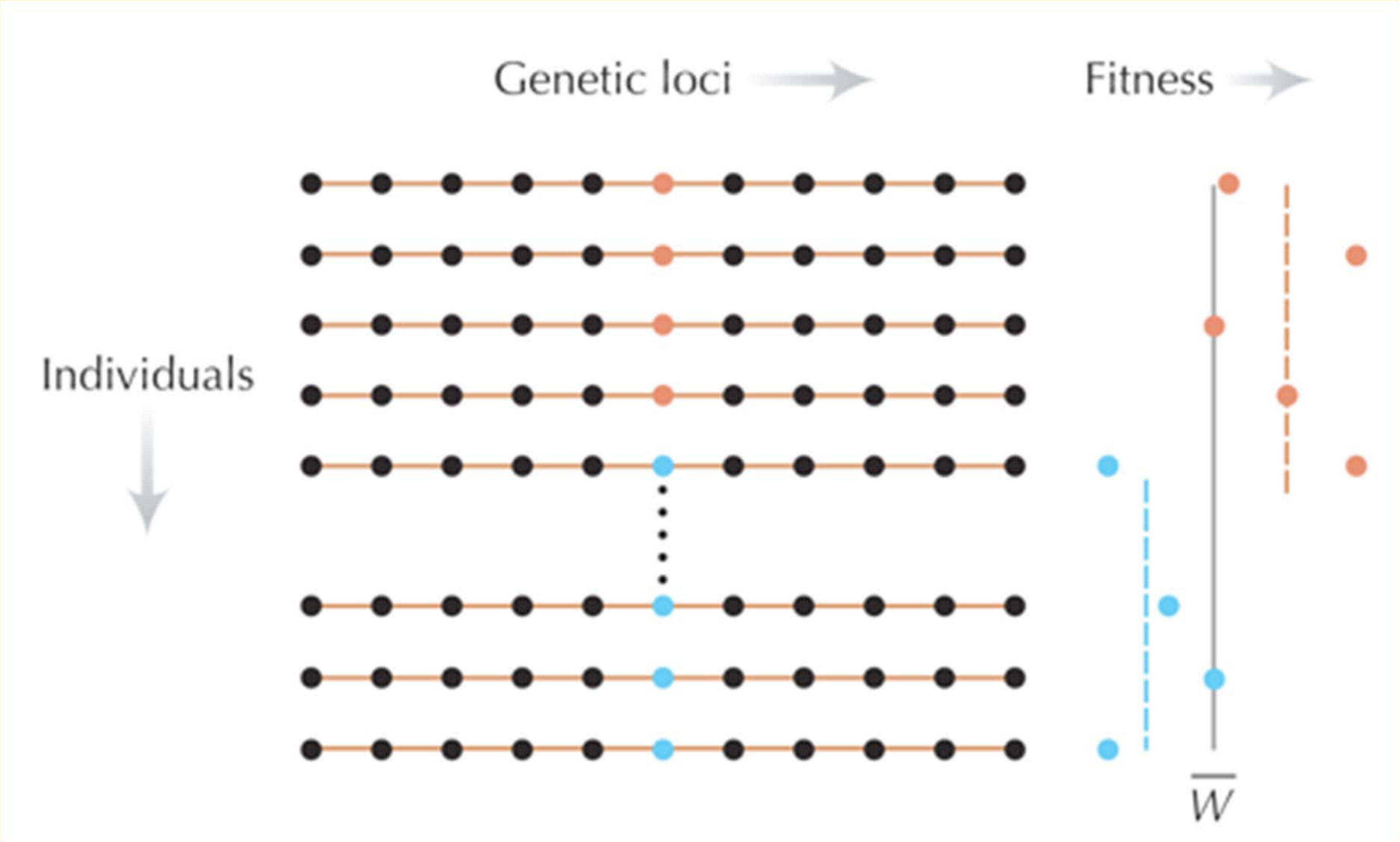
s: the selection coefficient



W (AA) = 1
W (Aa) = 1-0.38
W (aa) = 1-0.26

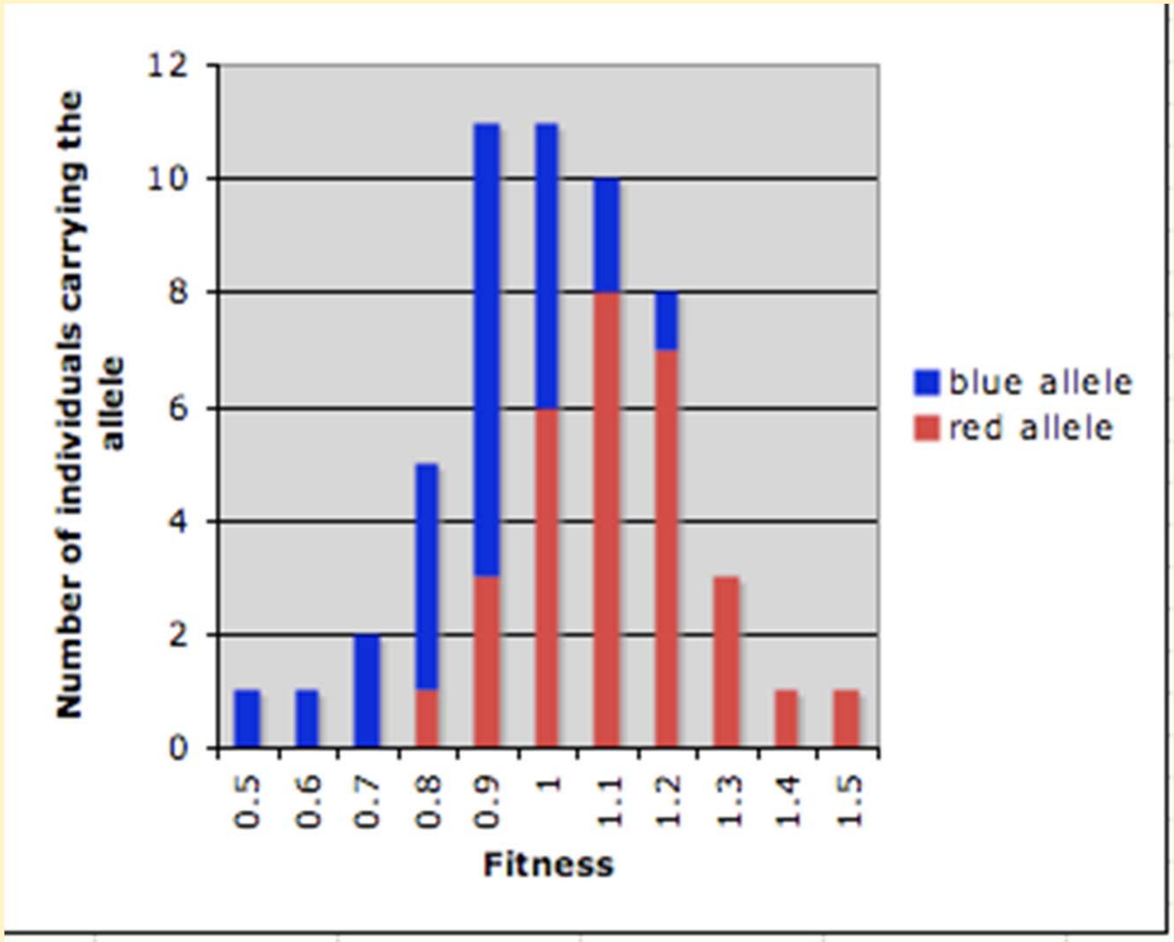
- One genotype's fitness is arbitrarily designated as 1

Fisher's fundamental theorem



- Each allele has an average fitness

Fisher's fundamental theorem



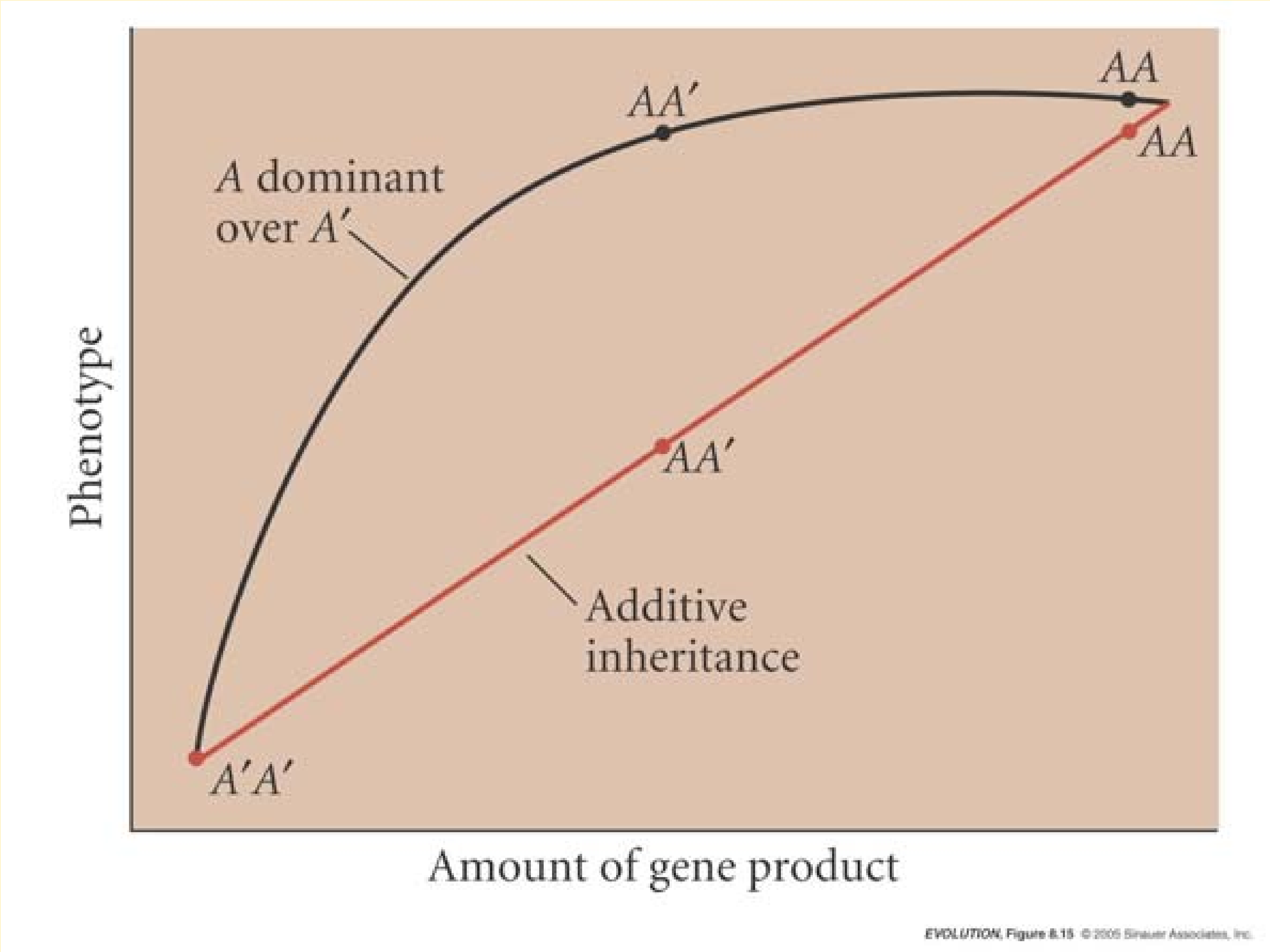
- What causes variation in fitness?

Fisher's fundamental theorem

$$\Delta\overline{W} = \mathrm{var}_A(W)/\overline{W}$$

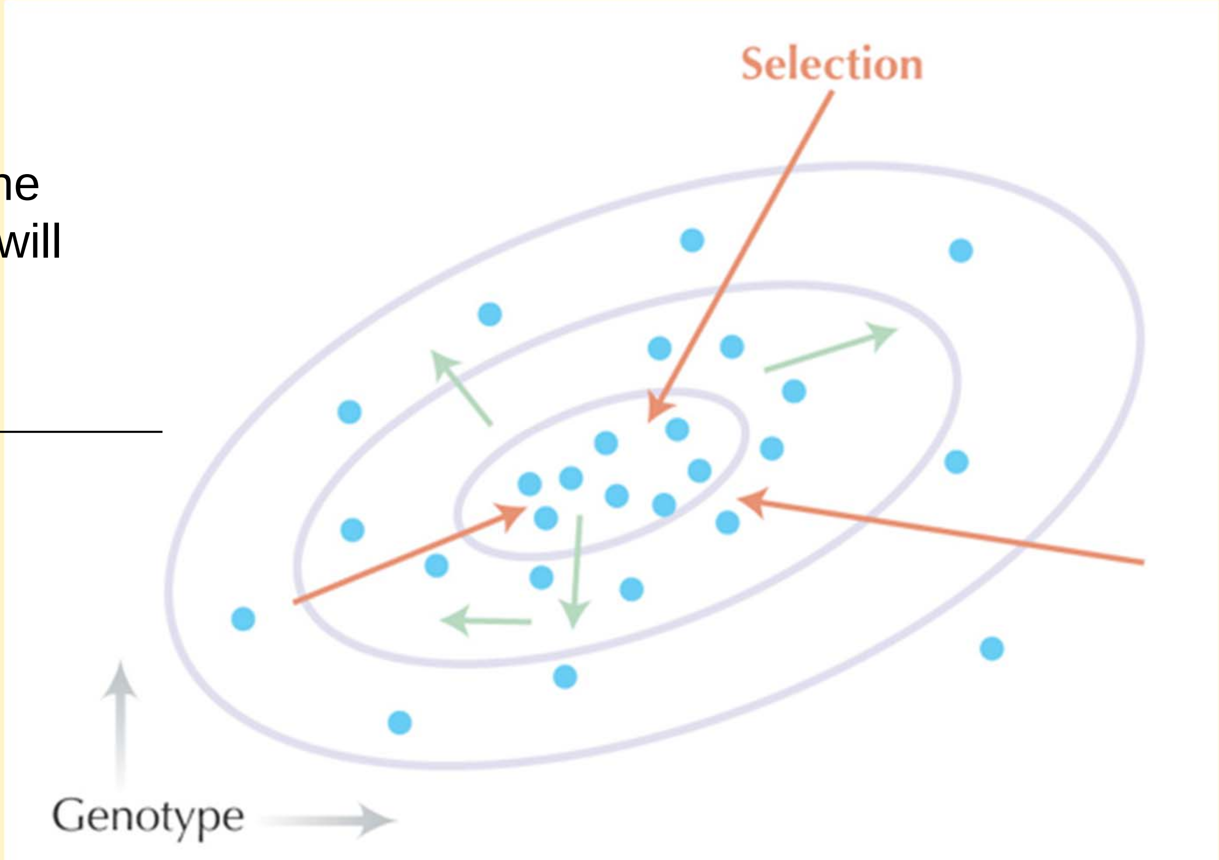
- The change in mean fitness of a population is due to the additive genetic variance in fitness divided by the current average fitness
- The higher the variance in fitness due to heritable additive factors the greater the effect of natural selection

Dominance leads to non-additive variance



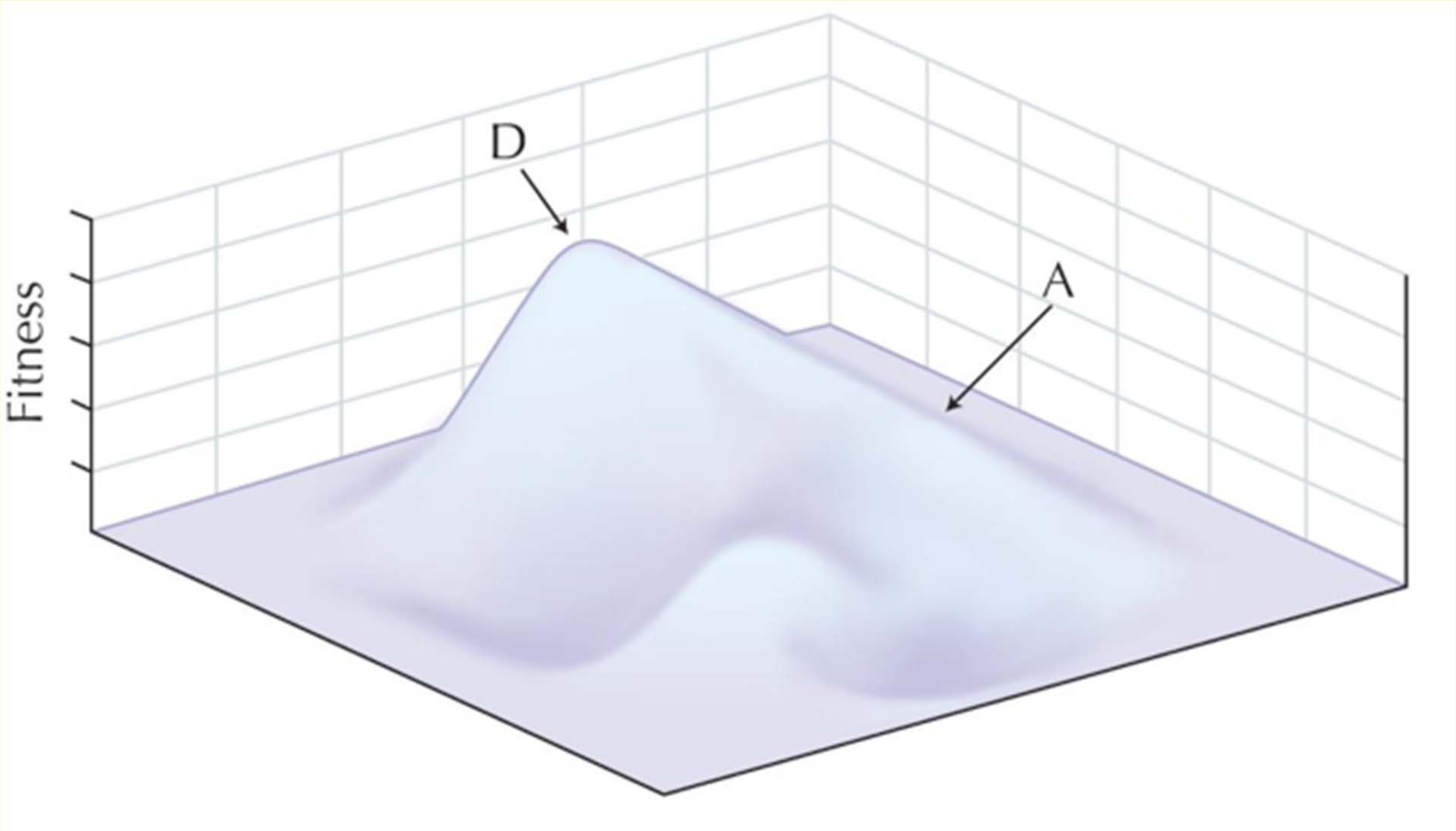
Other evolutionary processes counteract selection

Changes in the environment will change the optimum



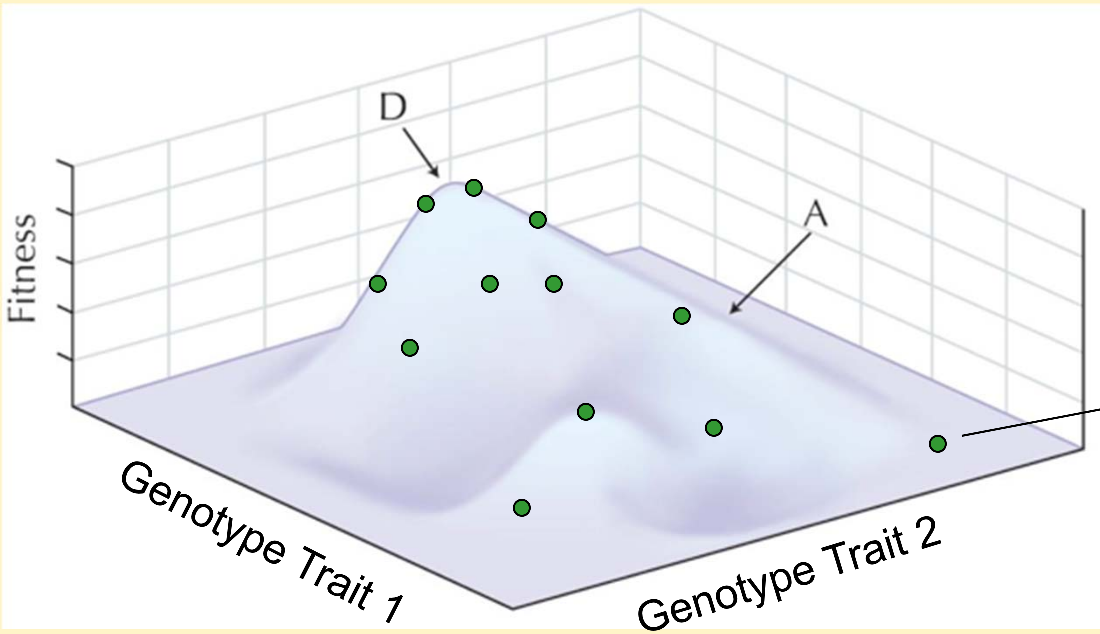
- Mutation, migration, and recombination counteract natural selection

Fitness landscapes



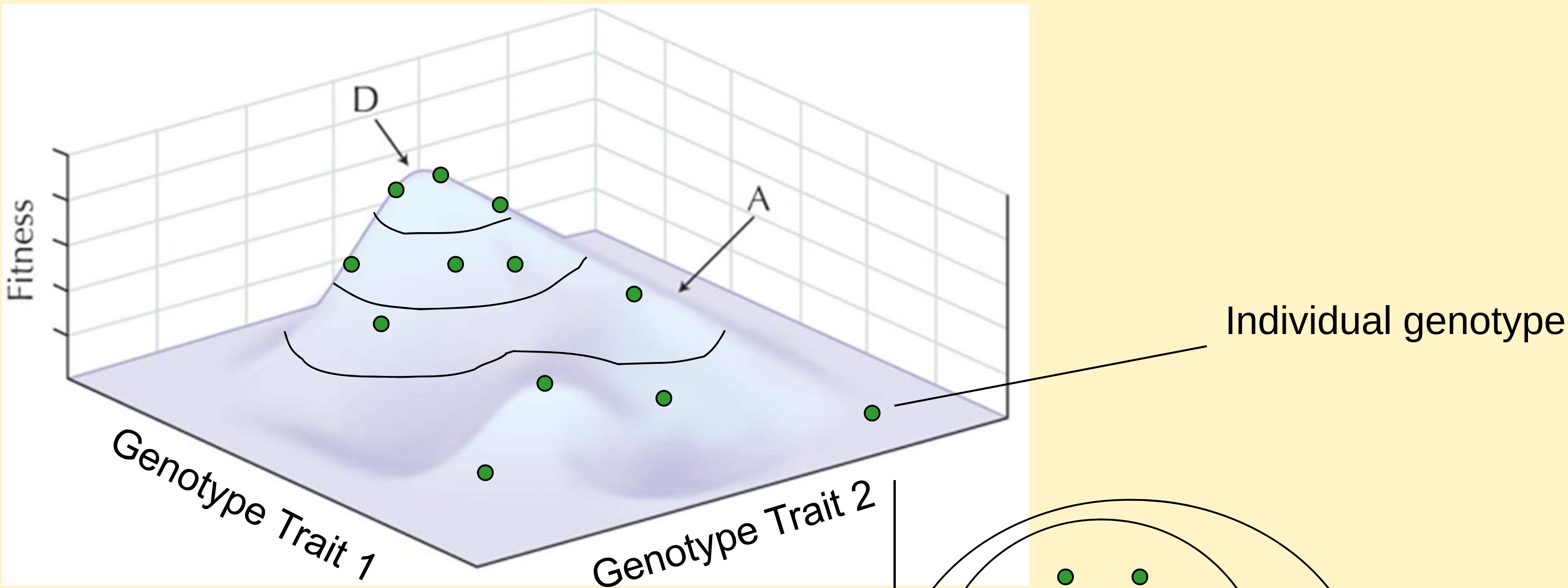
- Horizontal axes are genotype/allele/phenotype frequencies for two different loci/traits in a population

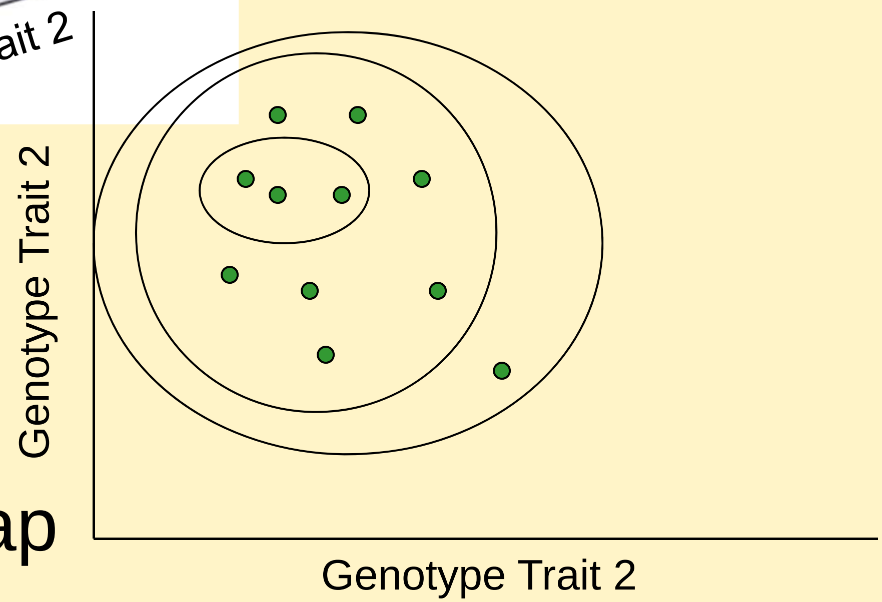
Fitness landscapes



Individual genotype

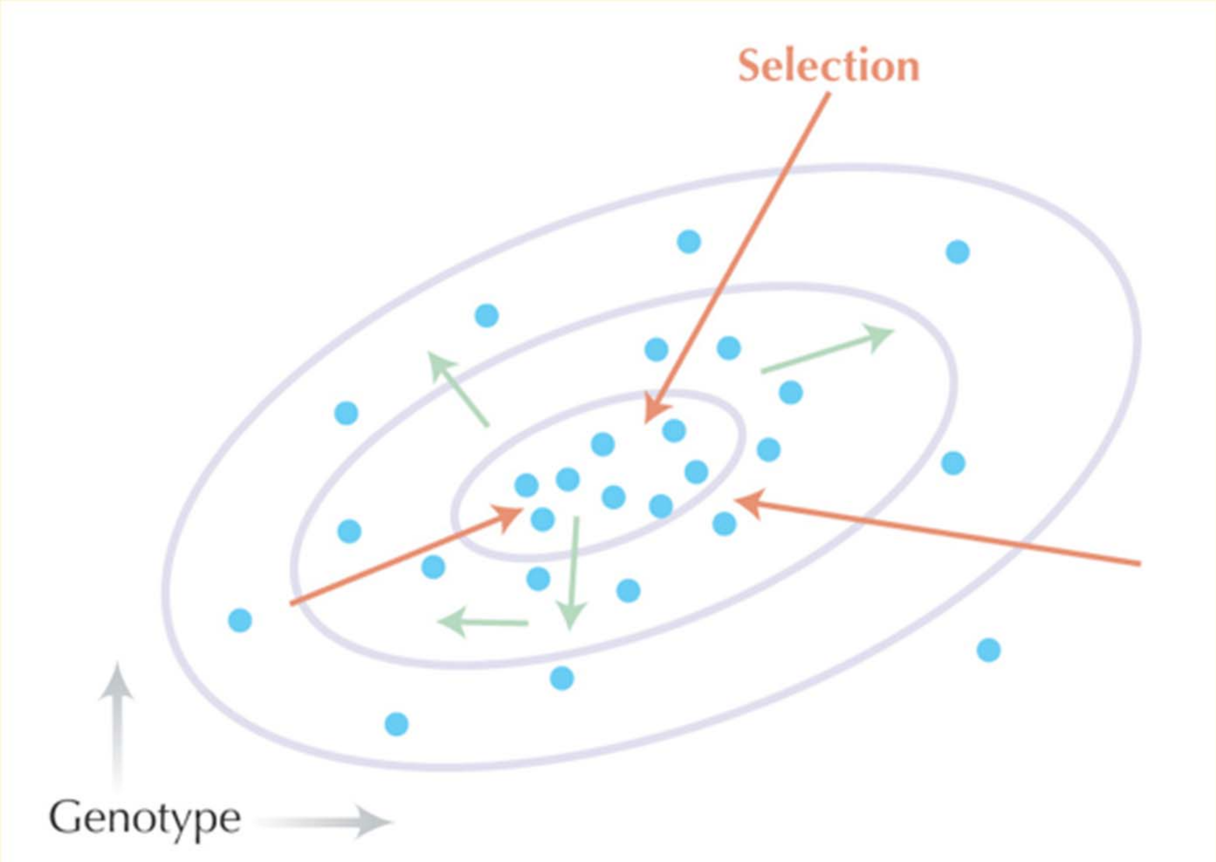
Fitness landscapes





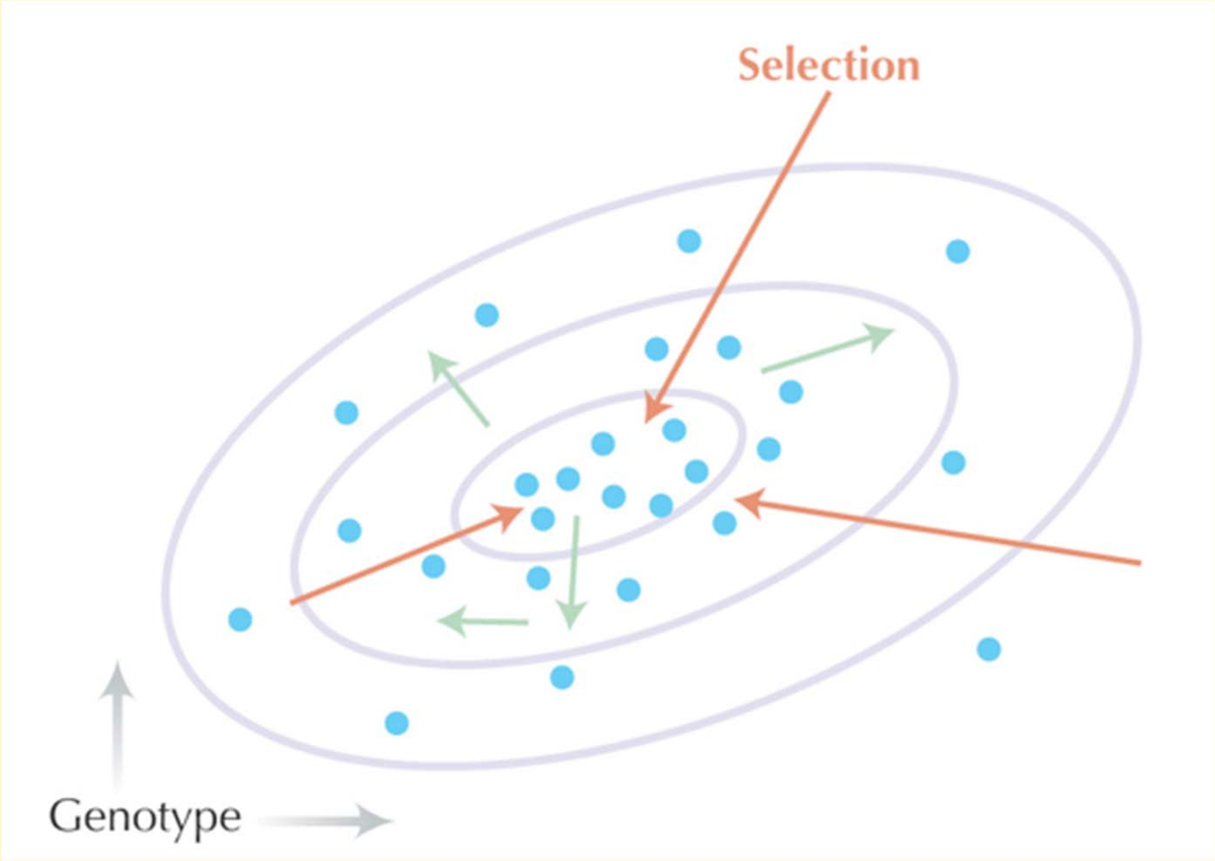
Translation into 2D
- similar to a topographic map

$$\Delta \overline{W} = \mathrm{var}_A(W)/\overline{W}$$

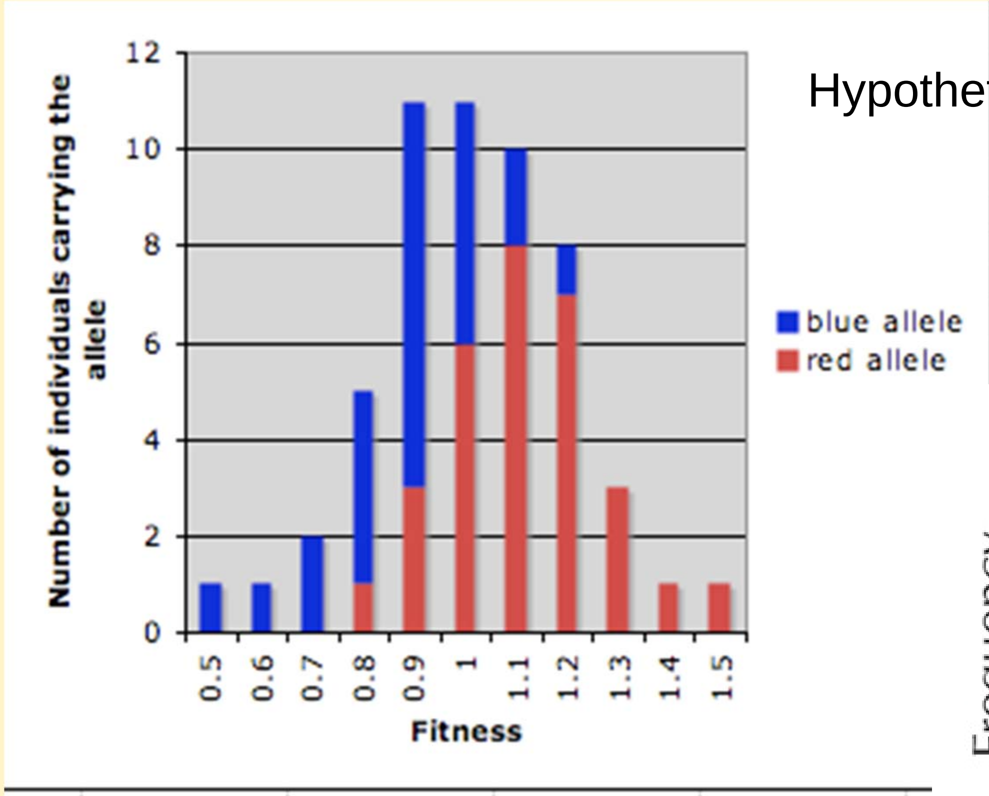


- What happens if average fitness and additive variance in fitness change?

Selection is the only process that leads to adaptation

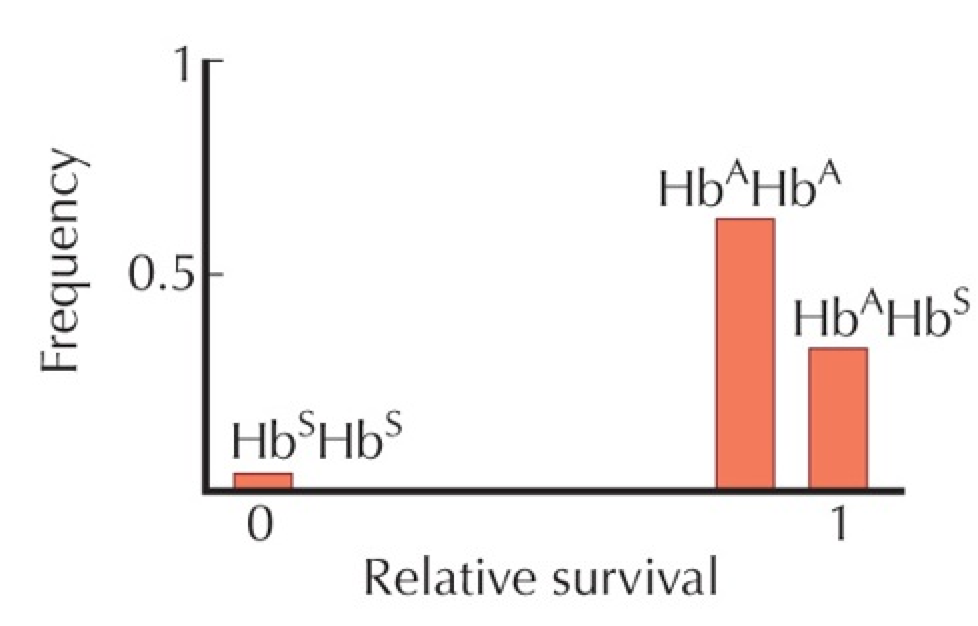


Fitness in quantitative and discrete traits



Hypothetical example

Sickle cell anemia



Modes of selection

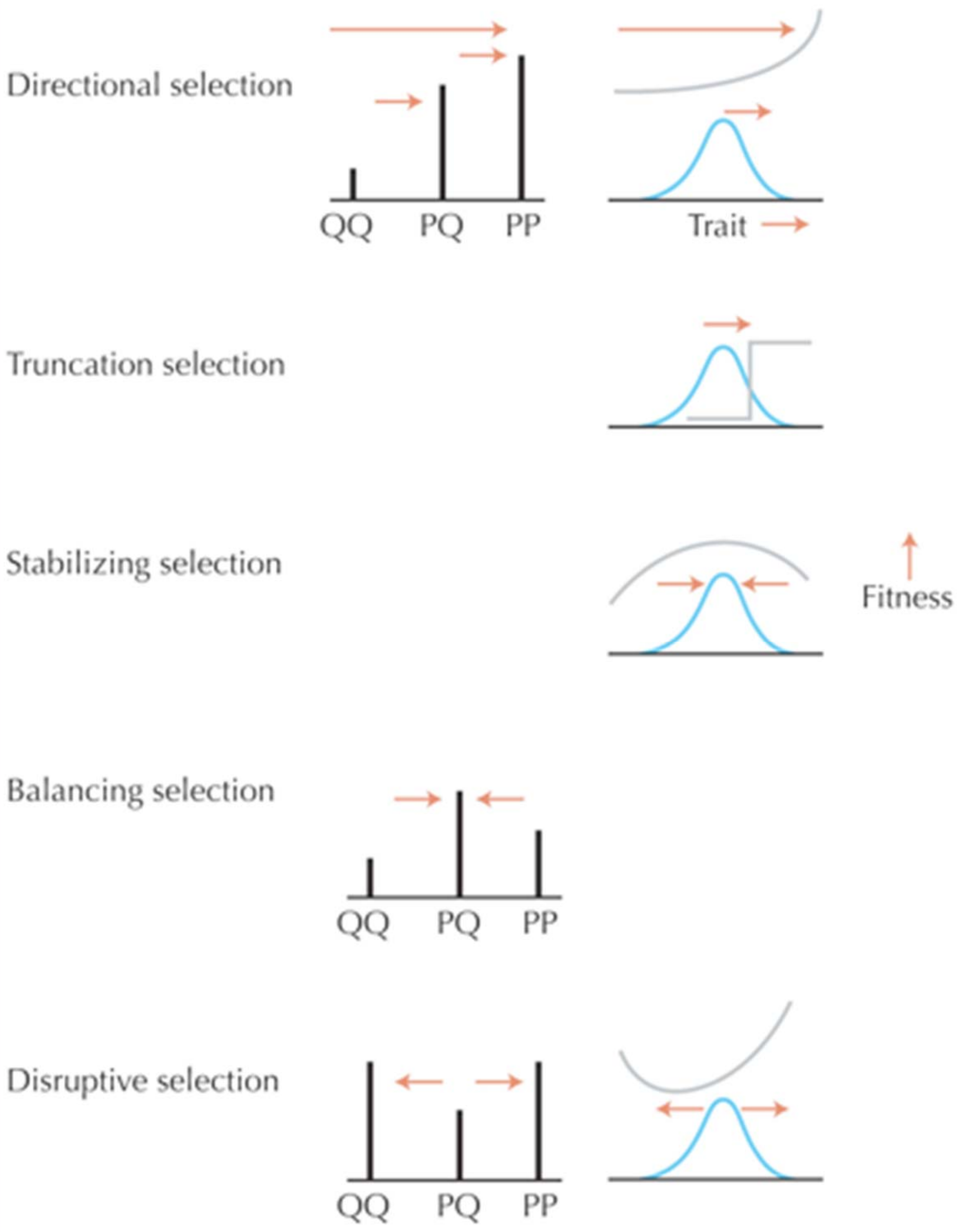


FIGURE BOX 17.2. Modes of Selection

Expected Genotype Frequencies in the Absence of Evolution are Determined by the Hardy-Weinberg Equation.

<u>Assumptions:</u>

1) No mutation
2) Random mating
3) Infinite population size
4) No immigration or emigration
5) No selection

Assumptions:

1) **No mutation**

2) **Random mating**

3) **Infinite population size**

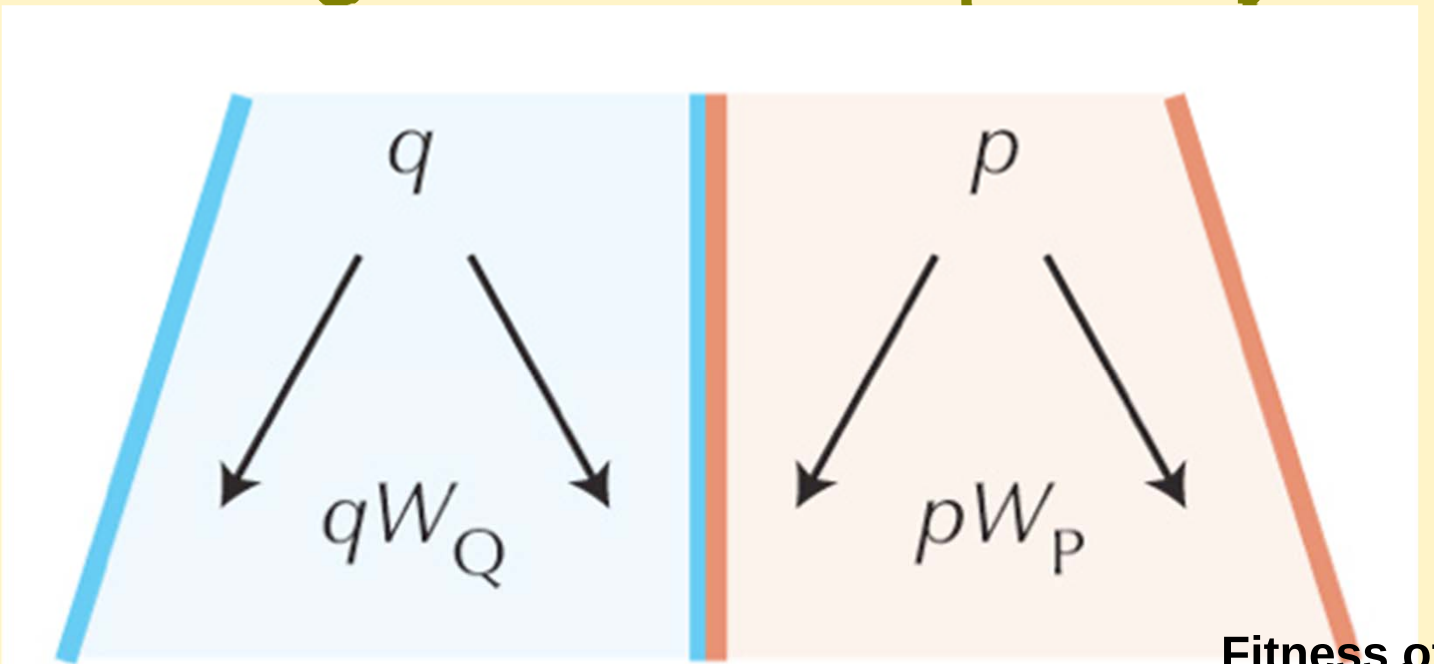
4) **No immigration or emigration**

5) **No selection**

Hardy-Weinberg equilibrium is the null-model of evolutionary biology:
No allele-frequency change = No evolution

How does the fitness of alleles change allele frequency?

t = 0



t = 1

Fitness of allele P

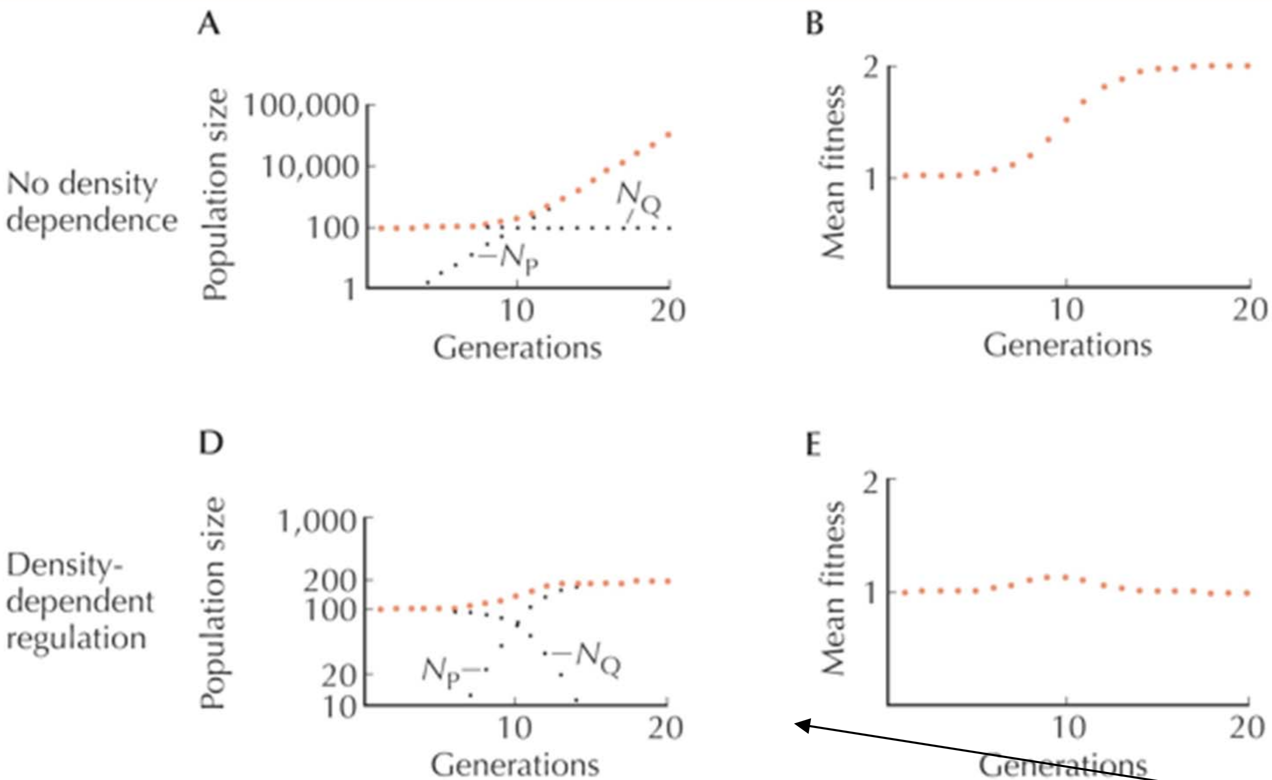
Number of copies of allele P (t=1)

- p and q are allele frequencies
- Is this case likely to be natural selection?

$$N_{P,1} = W_P N_{P,0}$$

$$N_{Q,1} = W_Q N_{Q,0}$$

Differences in the fitness of alleles will change allele frequency

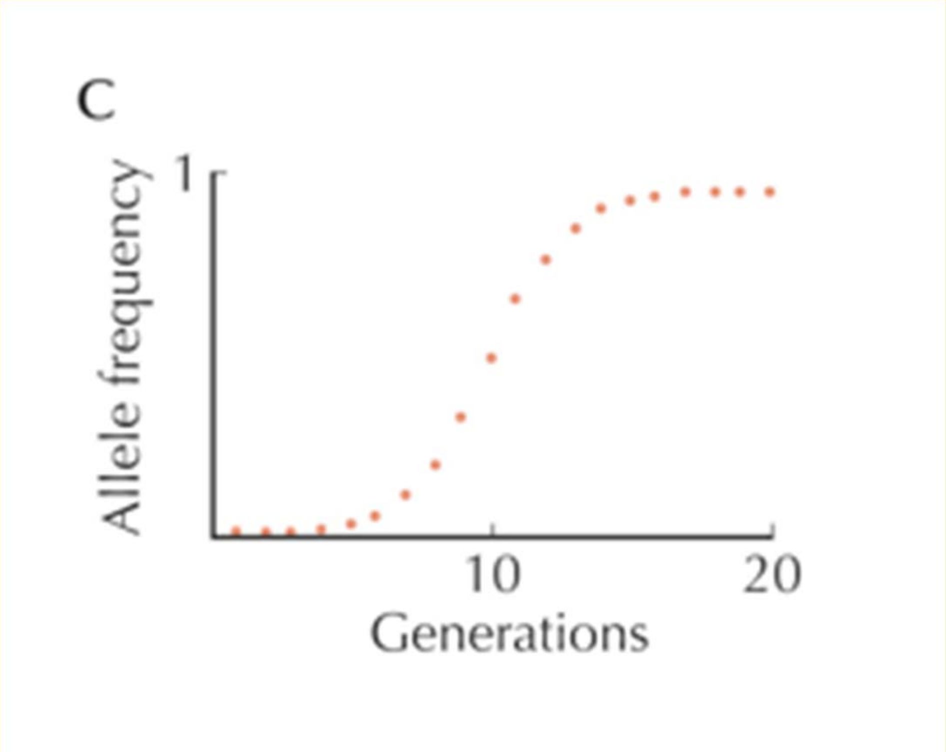


$W_P = 2 * W_Q$

Fitness of both alleles is equally effected by density

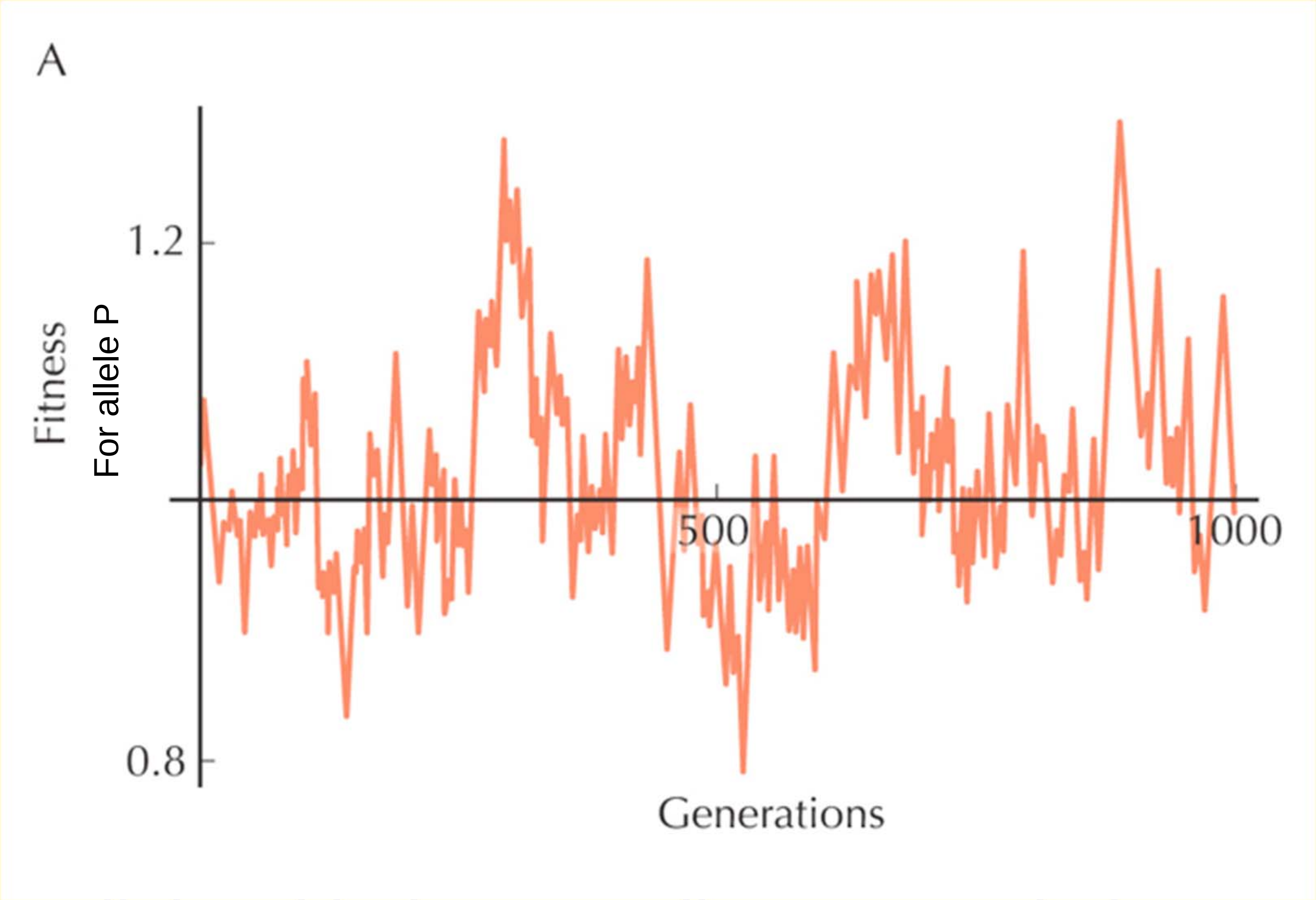
- Relative fitness is what matters!

Changes in allele frequency



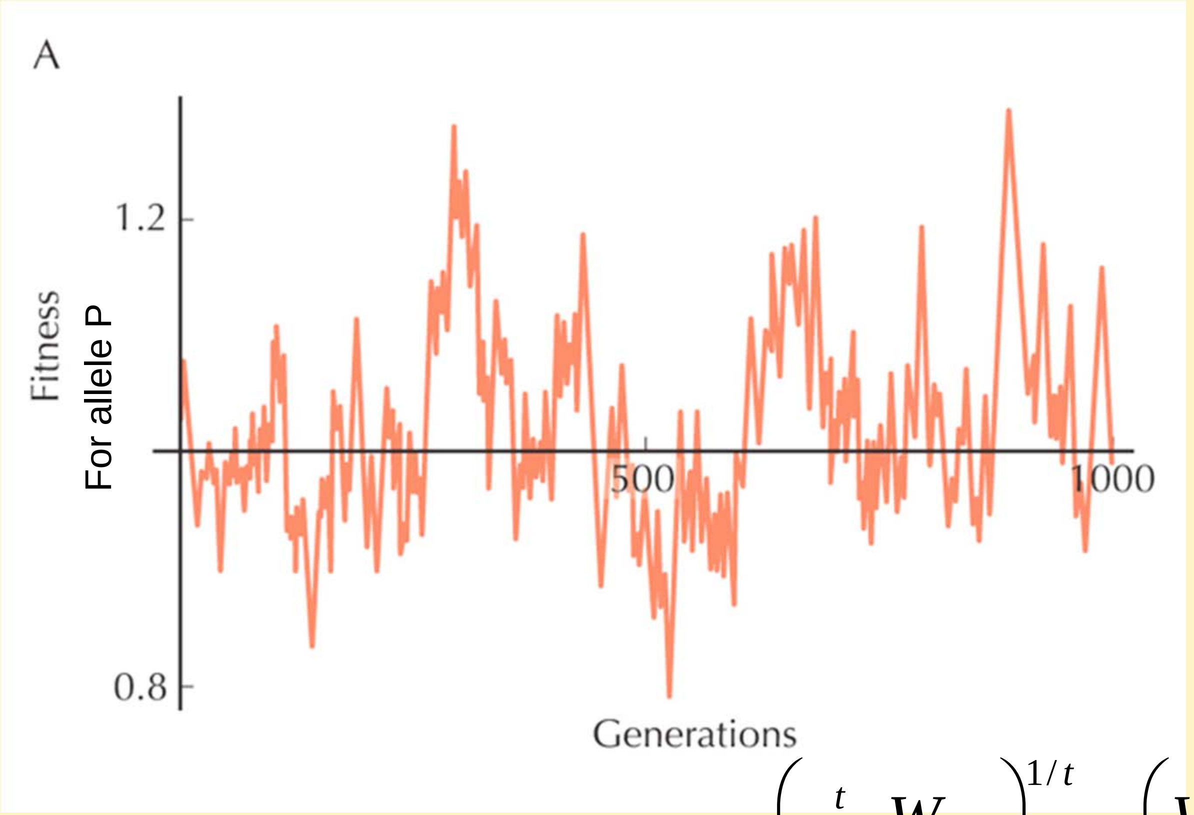
- Allele frequency changes in a sigmoid curve

What happens if the environment fluctuates?



- The allele with the overall greater relative fitness wins

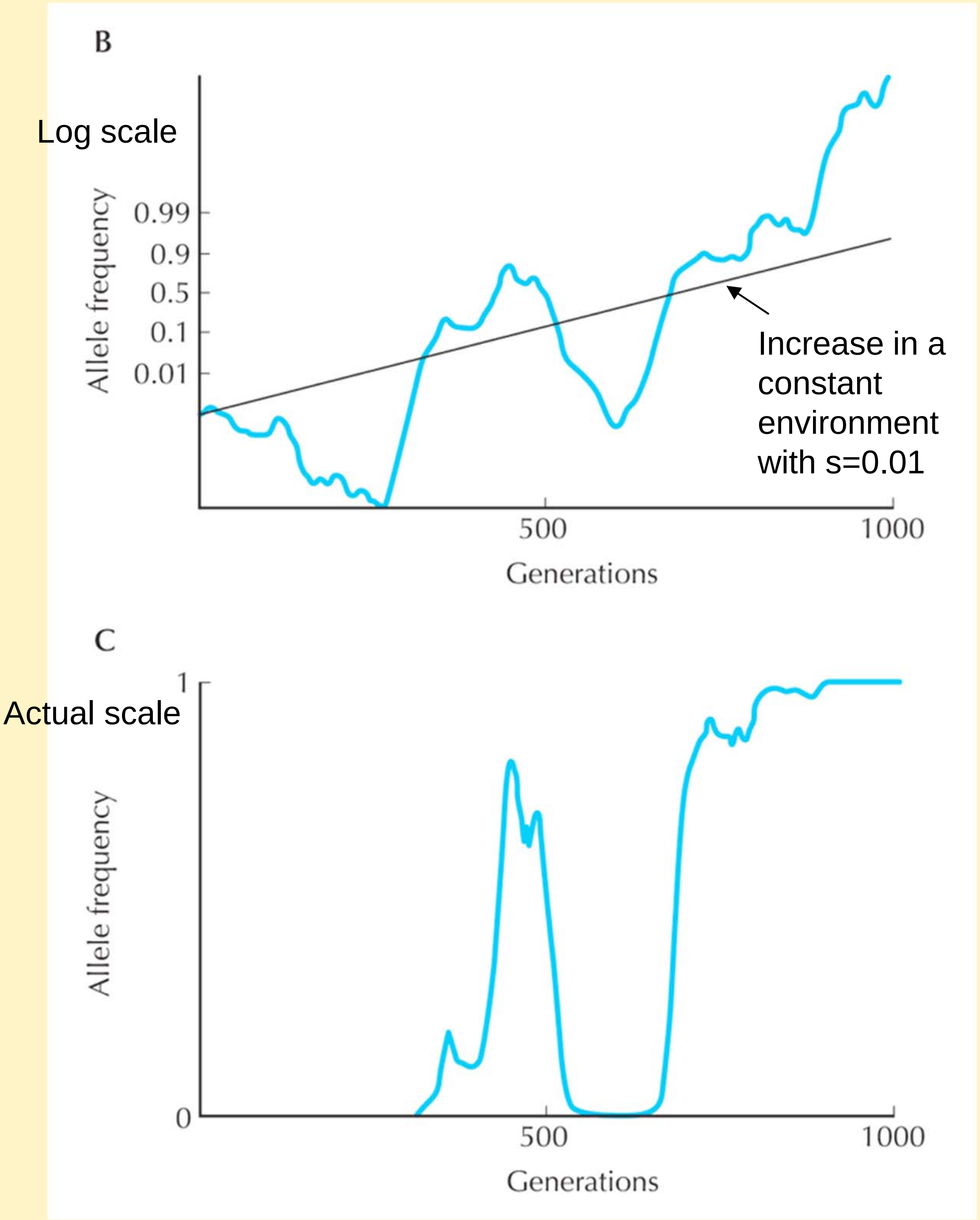
Geometric mean fitness



$$\left(\prod_{i=1}^{t}\frac{W_{P,i}}{W_{Q,i}}\right)^{1/t}=\left(\frac{W_{P,1}}{W_{Q,1}}\frac{W_{P,2}}{W_{Q,2}}\frac{W_{P,3}}{W_{Q,3}}\cdots\frac{W_{P,t}}{W_{Q,t}}\right)^{1/t}$$

- Geometric mean fitness for P=0.01

Increase is determined by a selective advantage of s=0.01



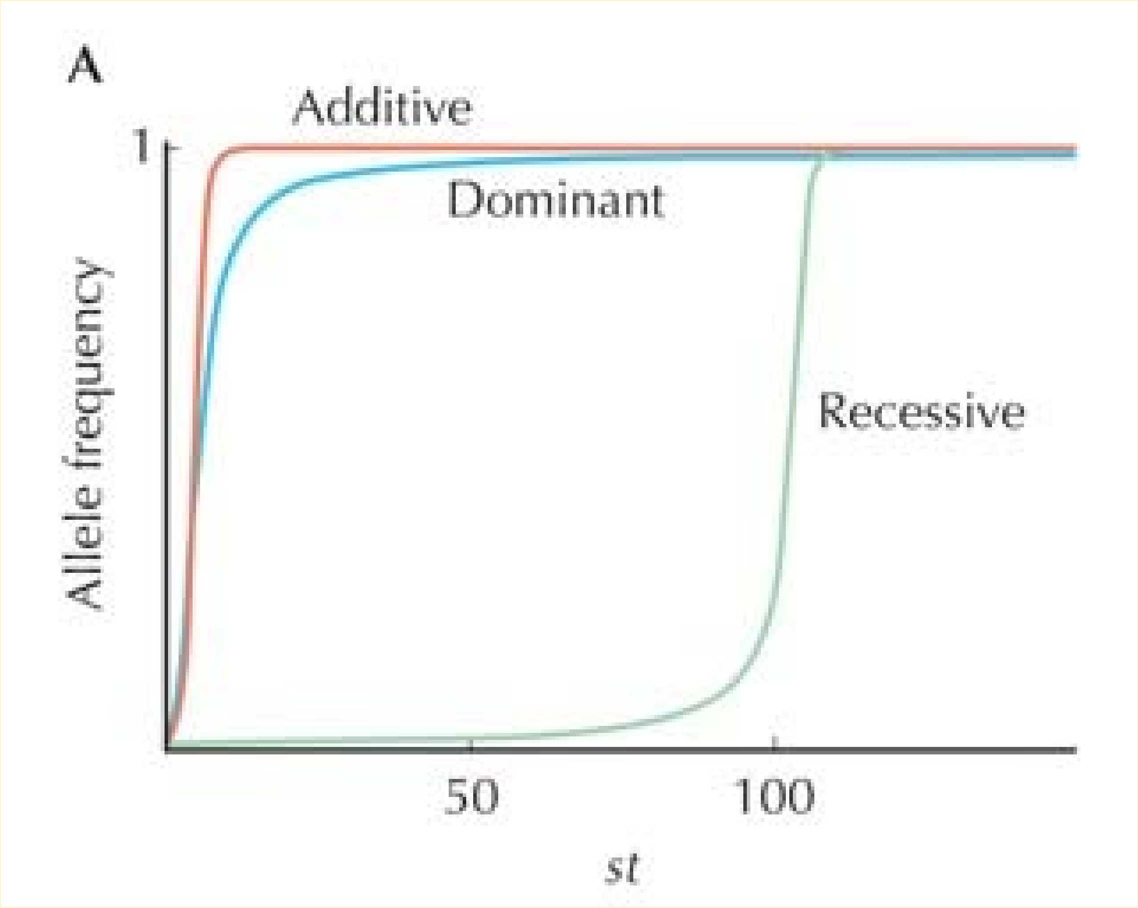
Interactions with other genes

- Interaction between homologous alleles in the same genotype

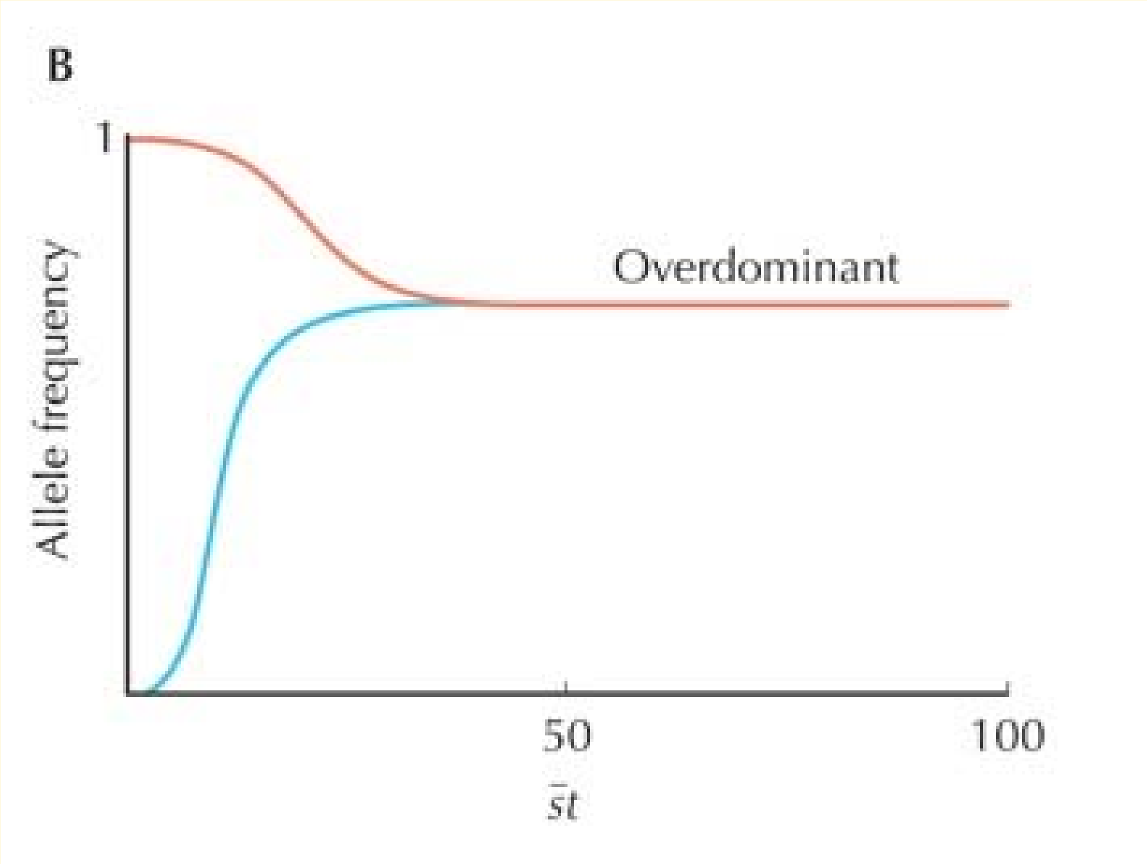
	Fitnesses of Diploid Genotypes		
	W_{QQ}	W_{PQ}	W_{PP}
Haploid			
Additive	$1 - s$	1	$1 + s$
Dominant P	1	$1 + s$	$1 + s$
Recessive P	1	1	$1 + s$
Overdominant	$1 - s_1$	1	$1 - s_2$
Underdominant	$1 + s_1$	1	$1 + s_2$

Directional selection

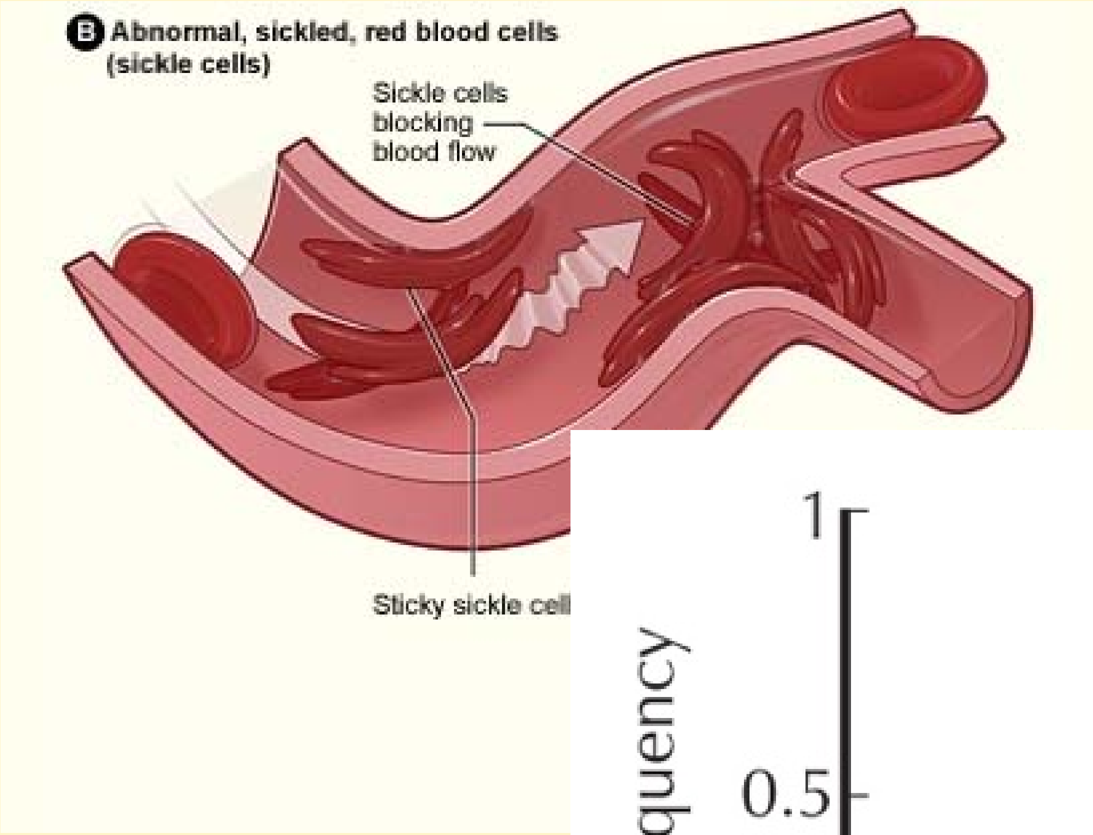
Directional selection

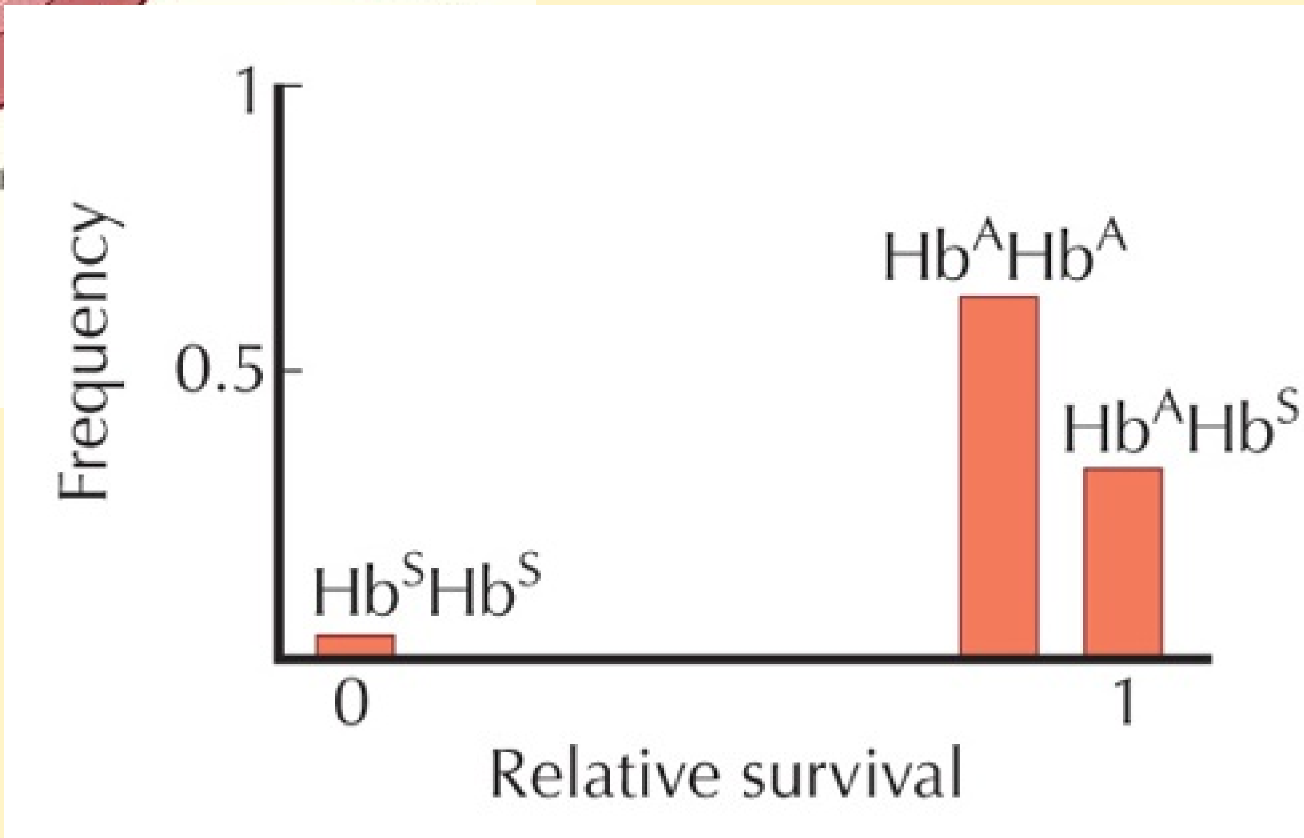


Overdominant selection

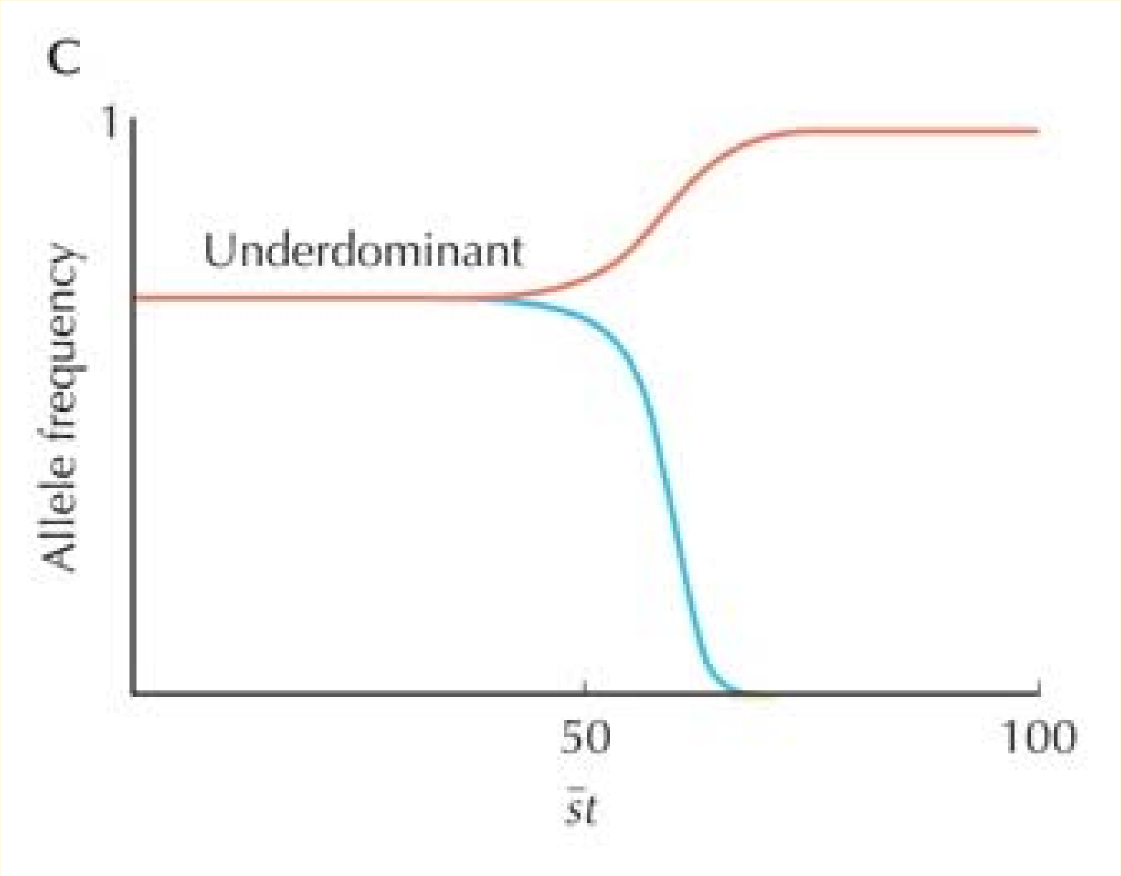


- E.g. sickle cell anemia



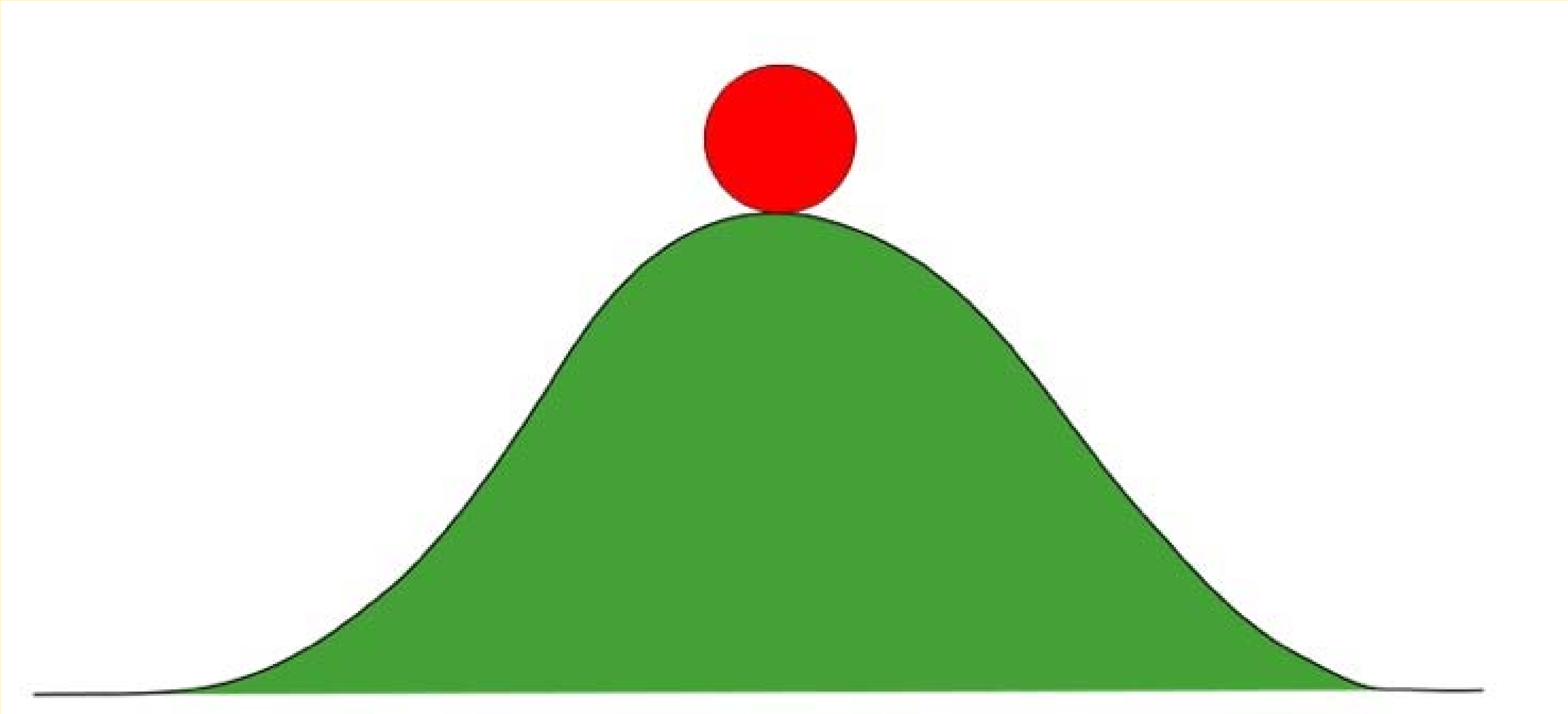


Underdominant selection



- Fitness is maximized at an unstable equilibrium

Unstable equilibrium



Split of the population into two different ecotypes

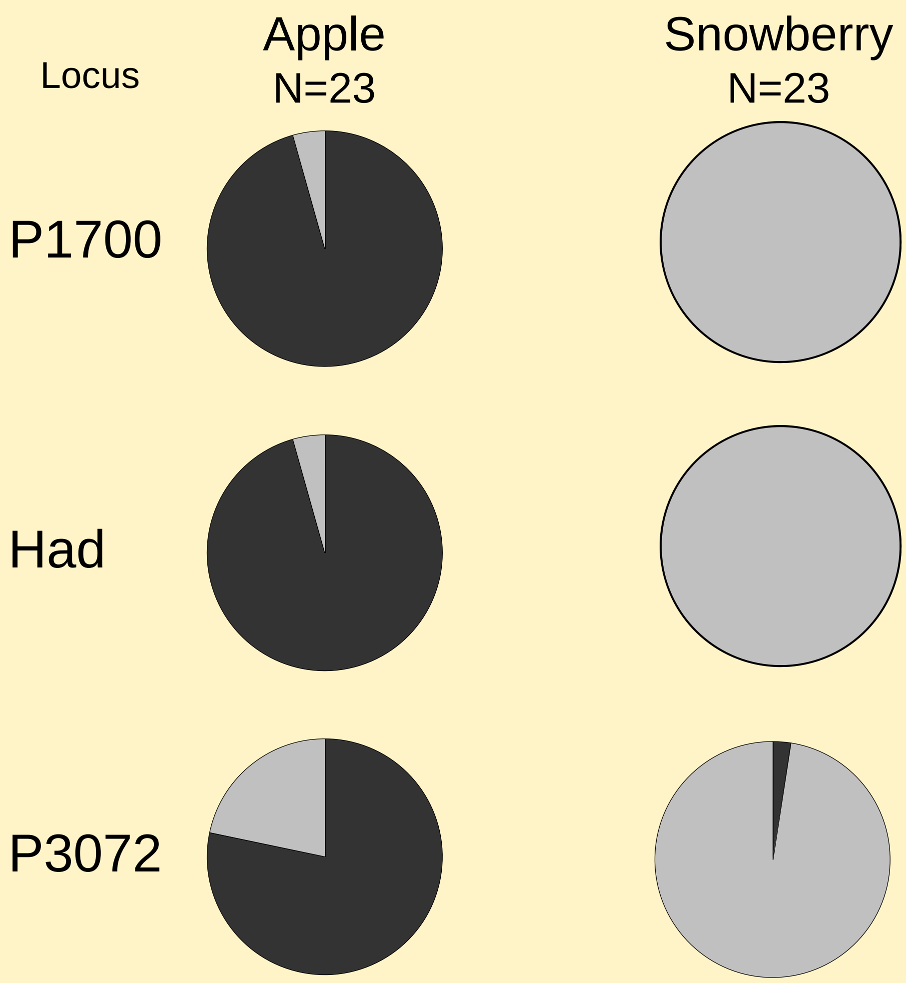
Apple maggots and snowberry maggots in Bellingham

Rhagoletis pomonella

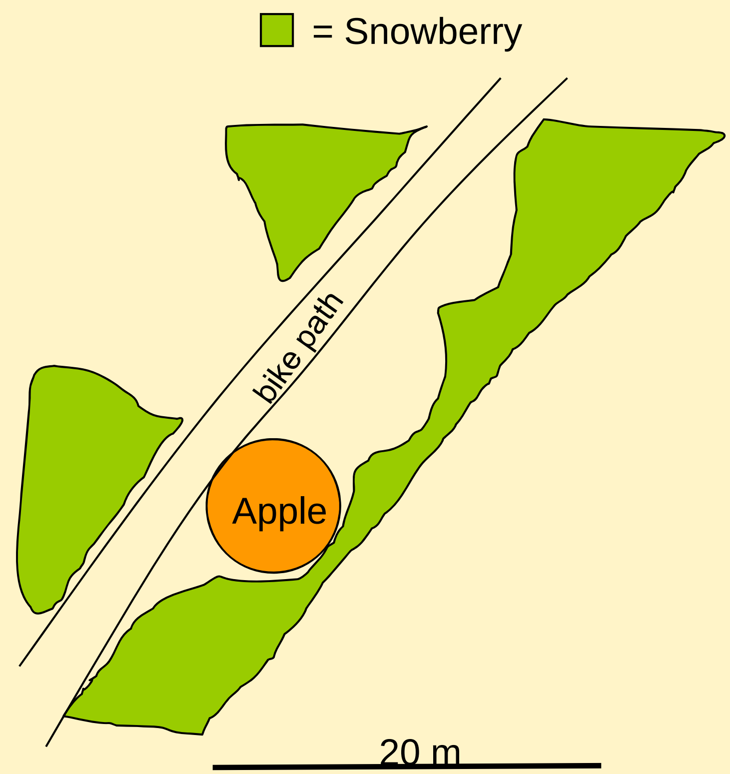
Sibling species, morphologically identical

Rhagoletis zephyria

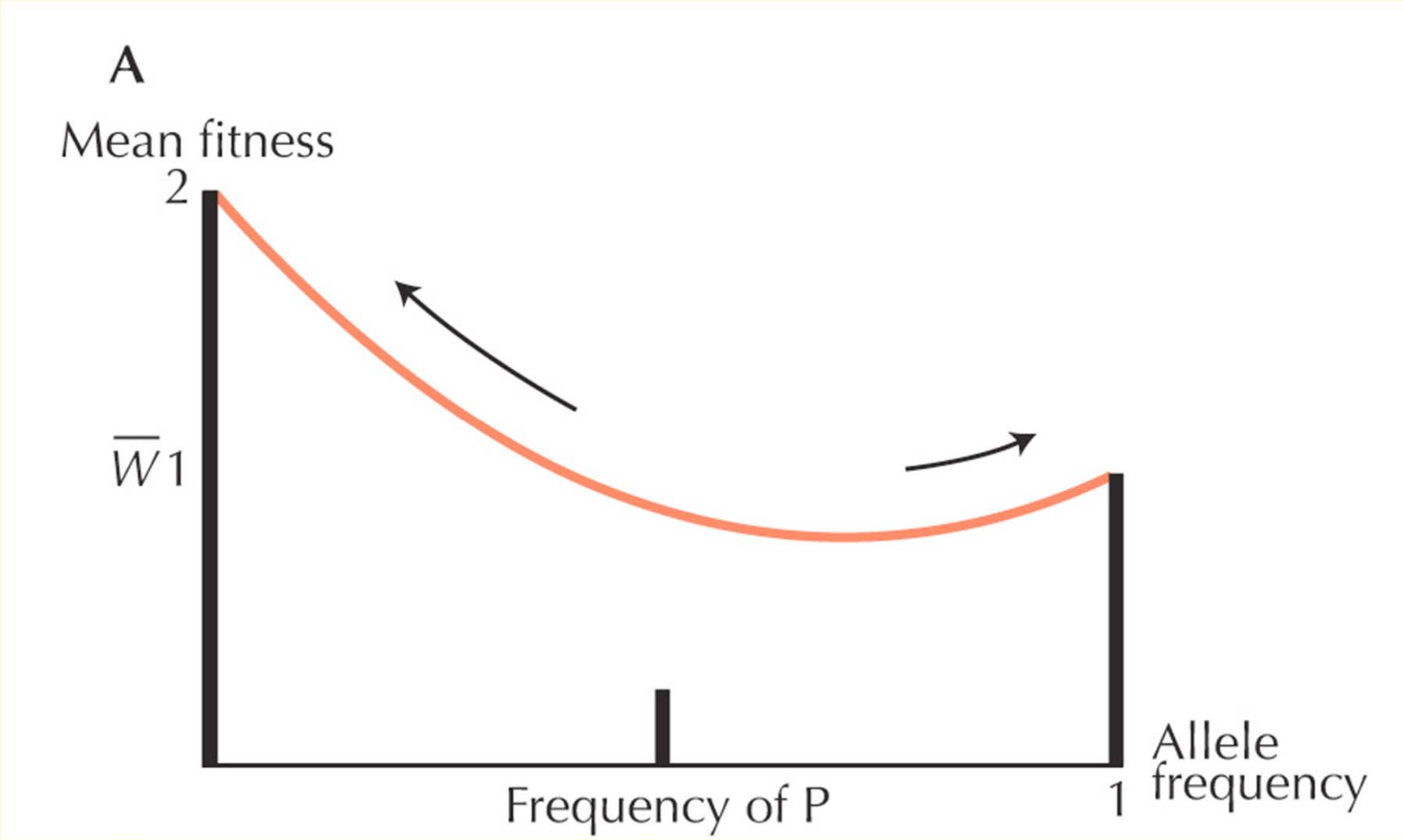
Allele frequencies at a micro-sympatric site along S. Bay trail, Bellingham, WA



= "*pomonella* allele"
= "*zephyria* allele"

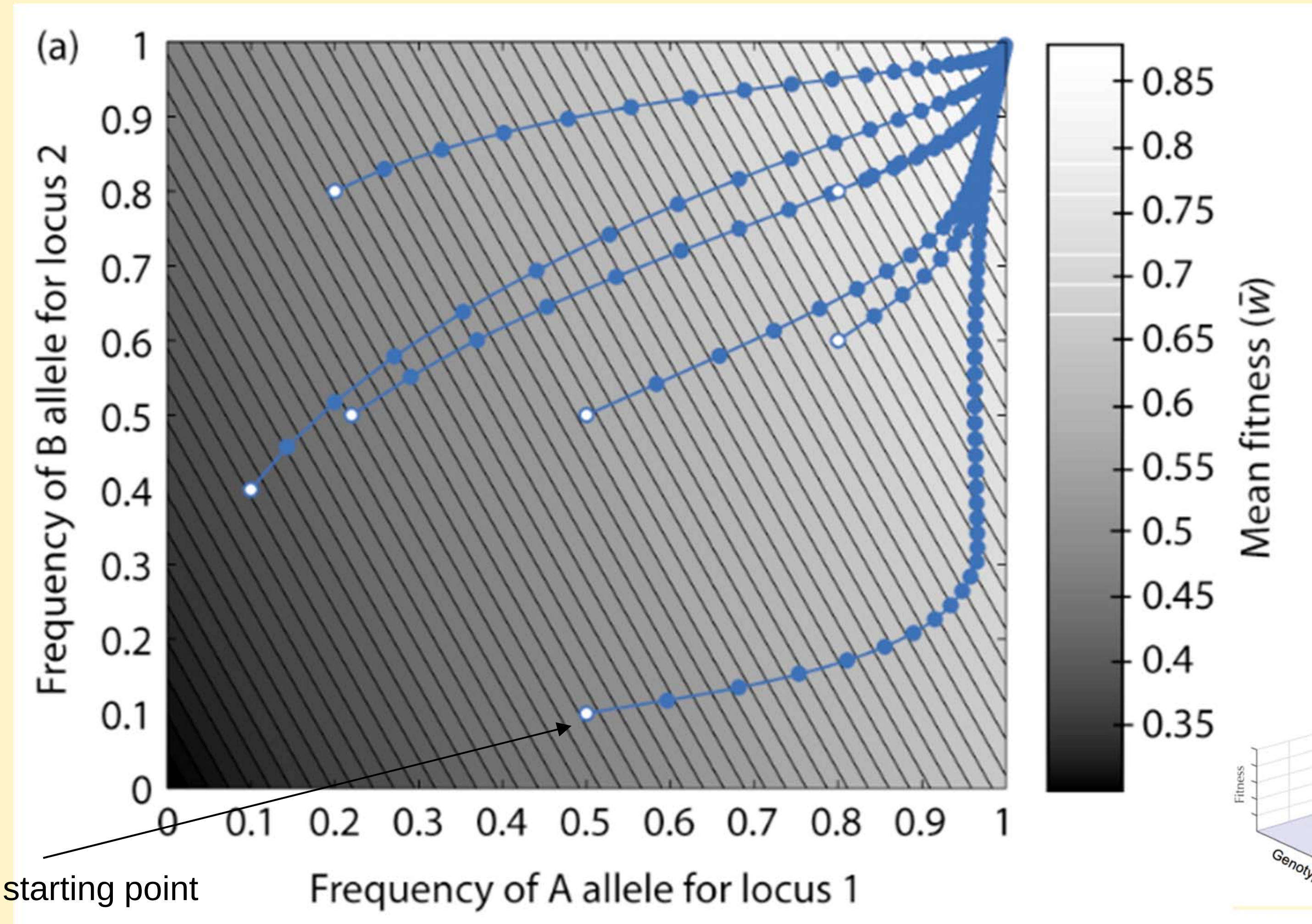


Fitness landscape make predictions about how selection will shift allele frequencies

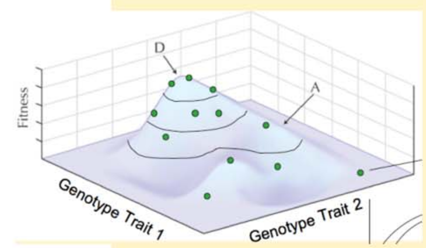


Interactions with other genotypes

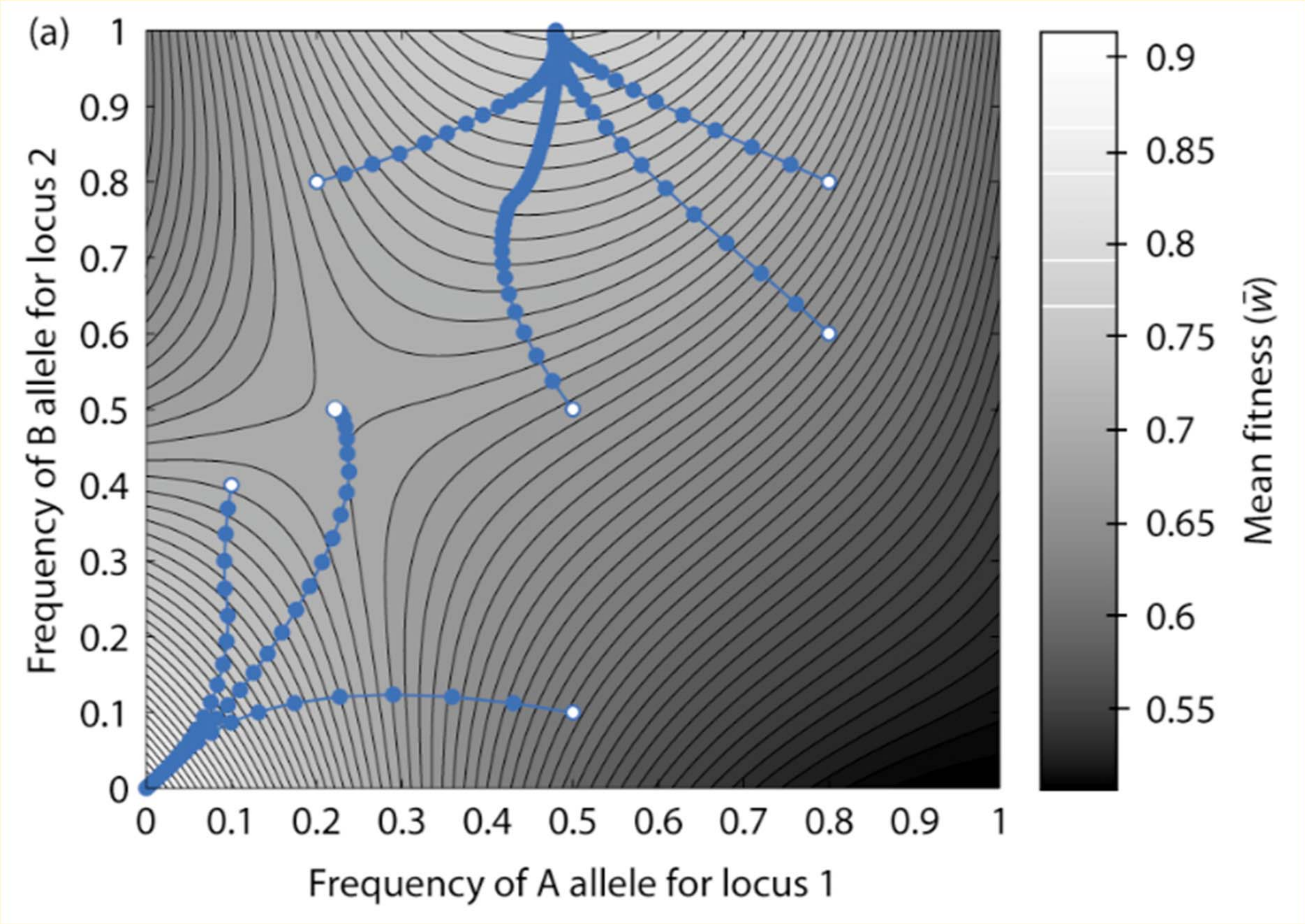
- Additive interaction between two loci

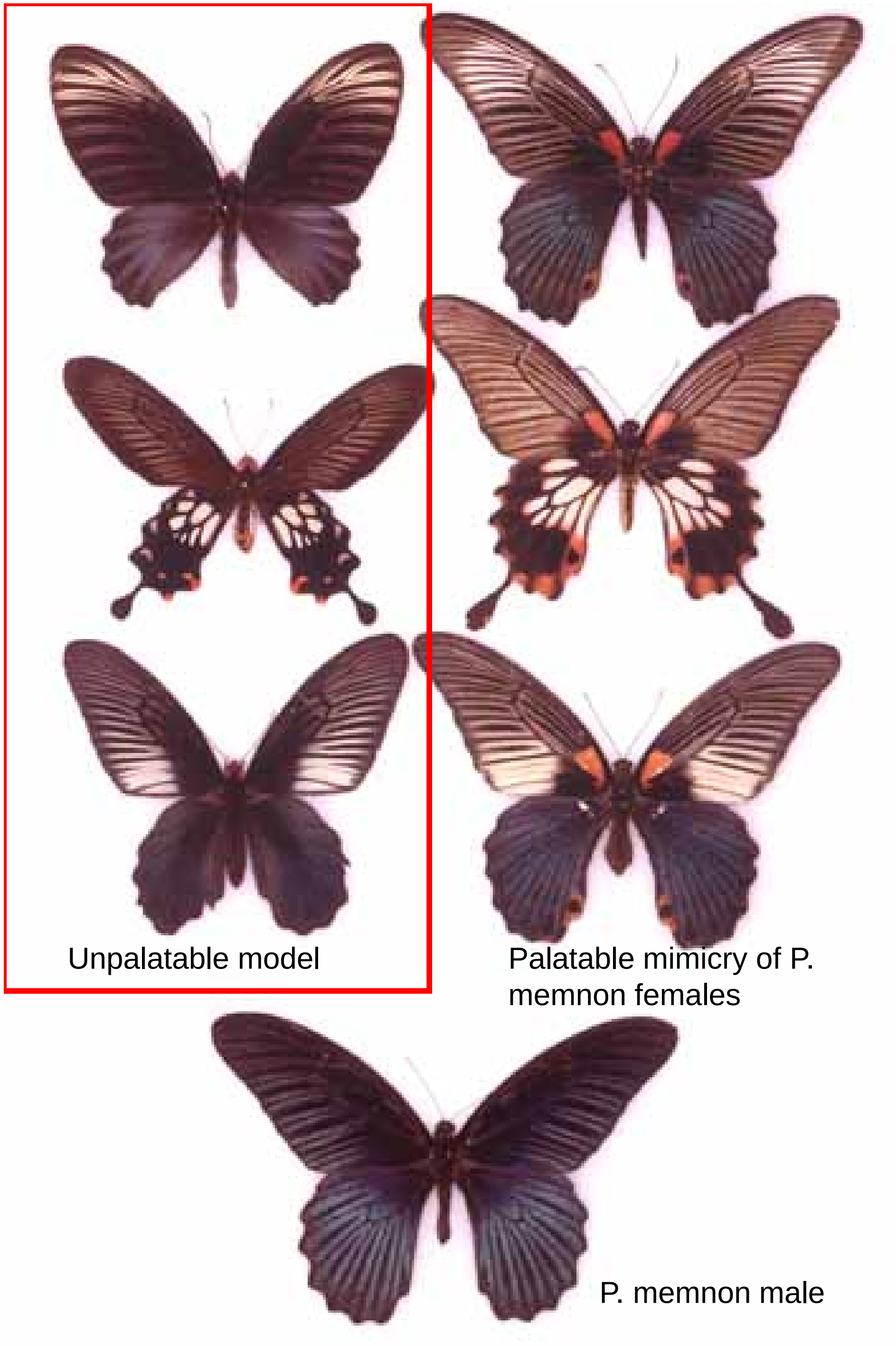


One starting point



Epistatic interaction



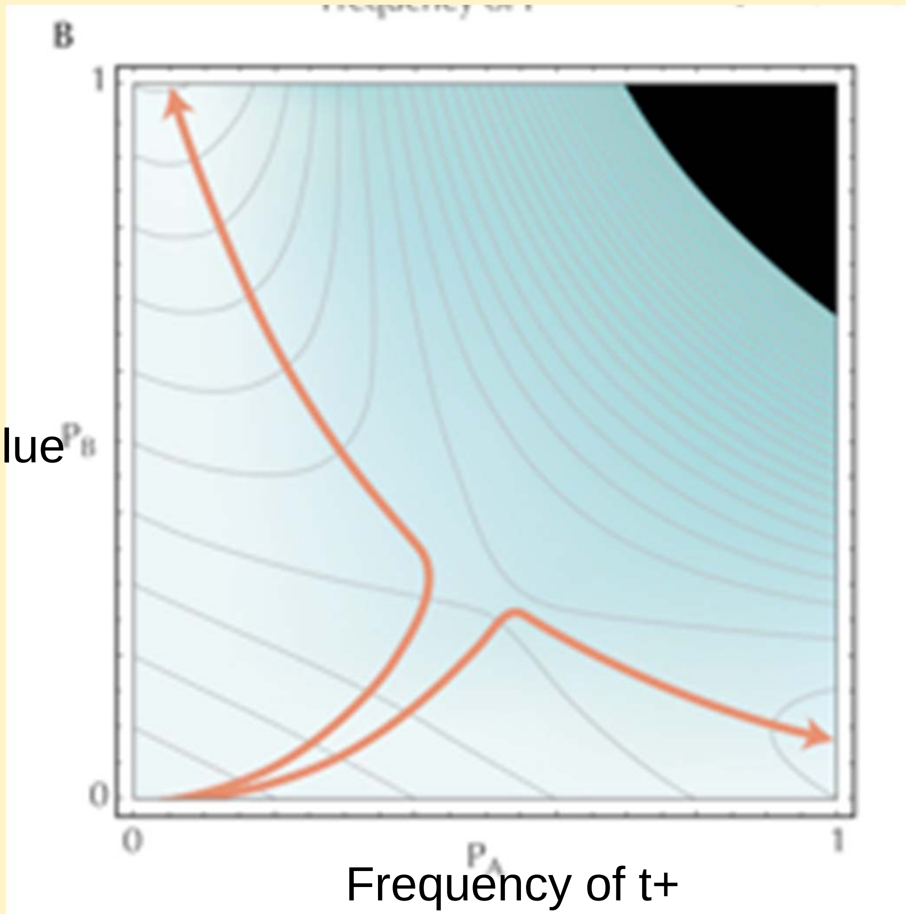


Epistatic interactions

- *Papilio memnon*
- 1st locus controls color of hindwing (c-blue,c-white)
- 2nd locus controls whether tail is formed or not (t+,t-)

Batesian mimicry = Mimic is palatable

Adaptive landscape



- I am cheating a bit for pedagogic purposes here. This example could involve frequency dependence and the fitness for allelic combinations is not necessarily fixed.

Interactions with the environment

- With the environment
  - Density-dependent selection: Density affects different genotypes in a different manner
  - Frequency-dependent selection: Fitness depends on the relative frequencies of other genotypes

Müllerian Mimicry leads to frequency dependent selection

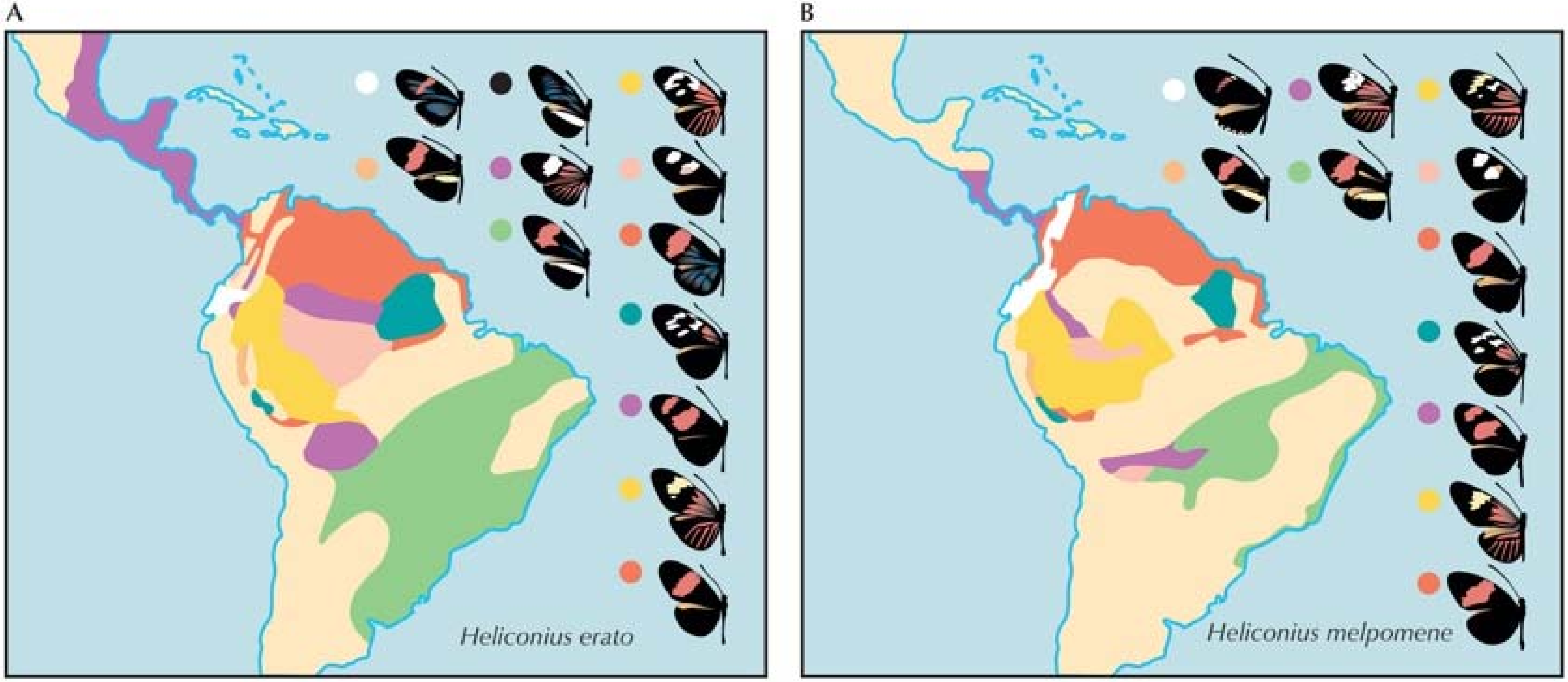
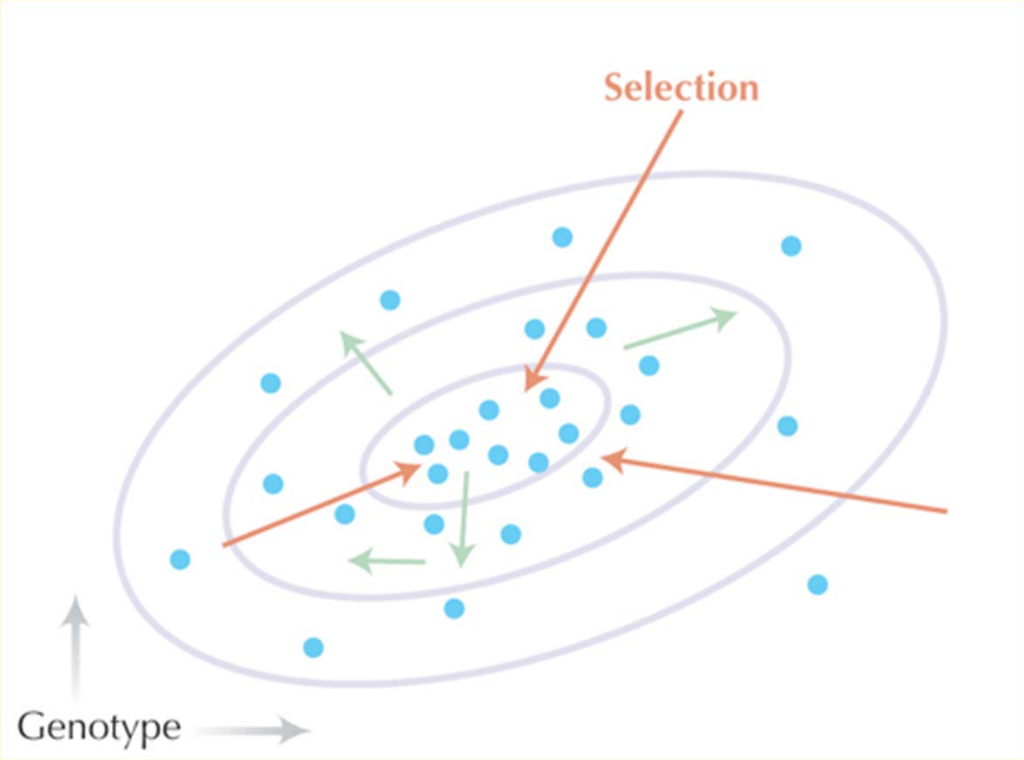


FIGURE 17.23. Müllerian mimicry in *Heliconius* butterflies. Within any one area, *Heliconius erato* (*A*) and *H. melpomene* (*B*) share the same warning pattern. However, patterns differ considerably across South and Central America.

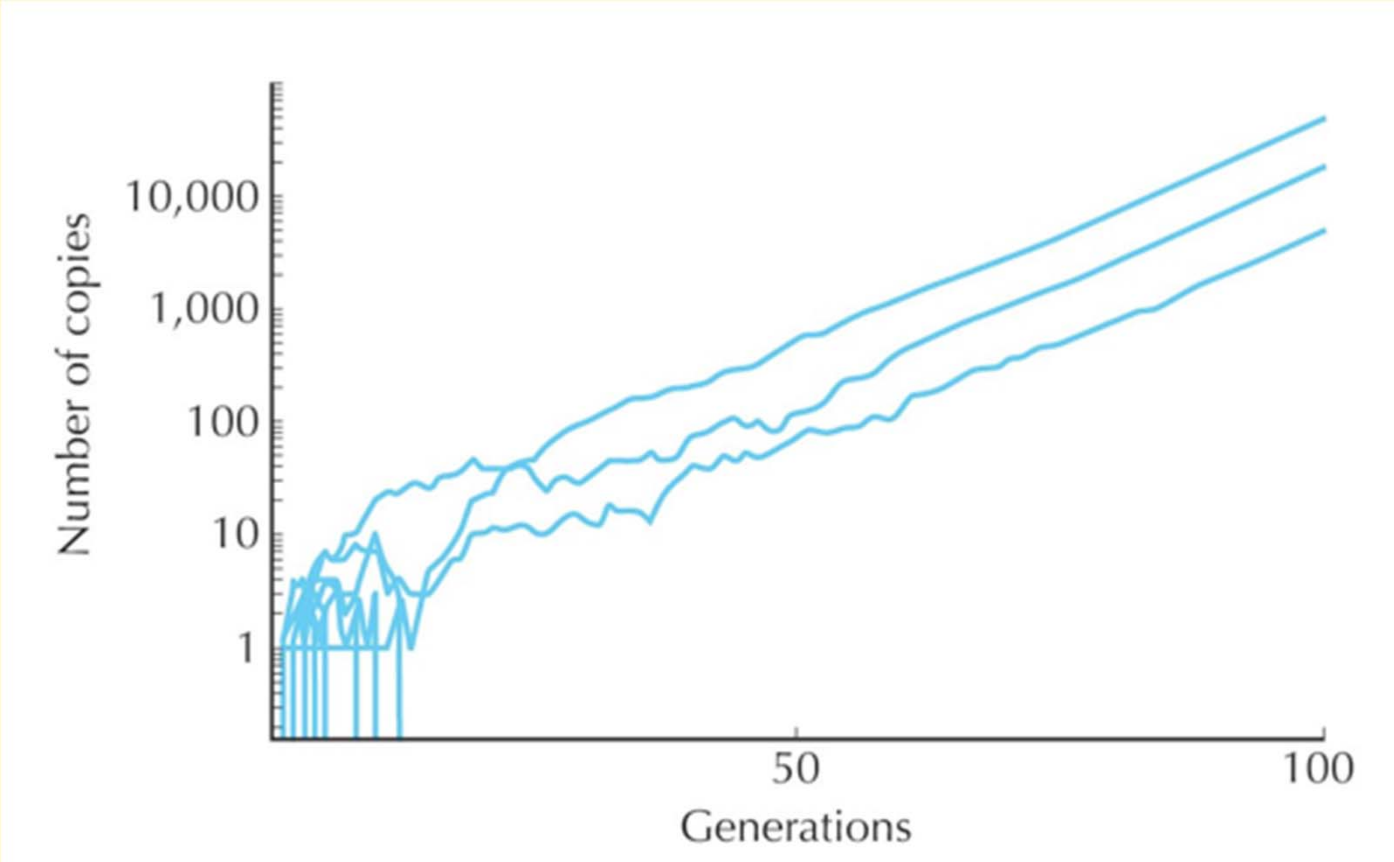
Müllerian Mimicry = Model and mimic are unpalatable

Interaction between selection and other forces

- Fundamental evolutionary processes
  - Mutation
  - Recombination
  - Gene flow
  - Random Drift
  - Selection



Random drift and selection

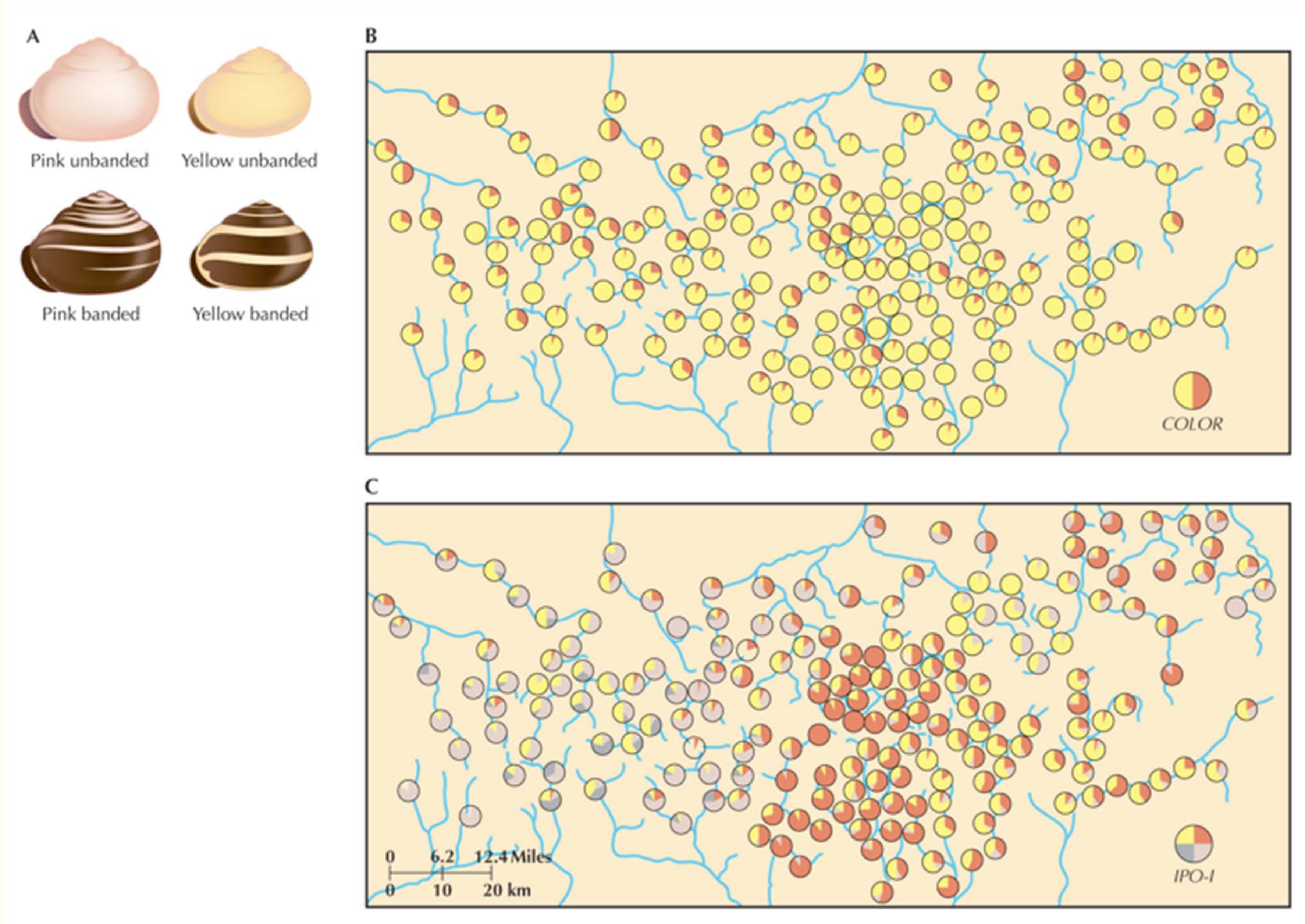


- Joint model of drift and selection
  - Most favorable alleles (27/30) go extinct when they are rare
  - Probability of survival for a single copy is ca. 2s

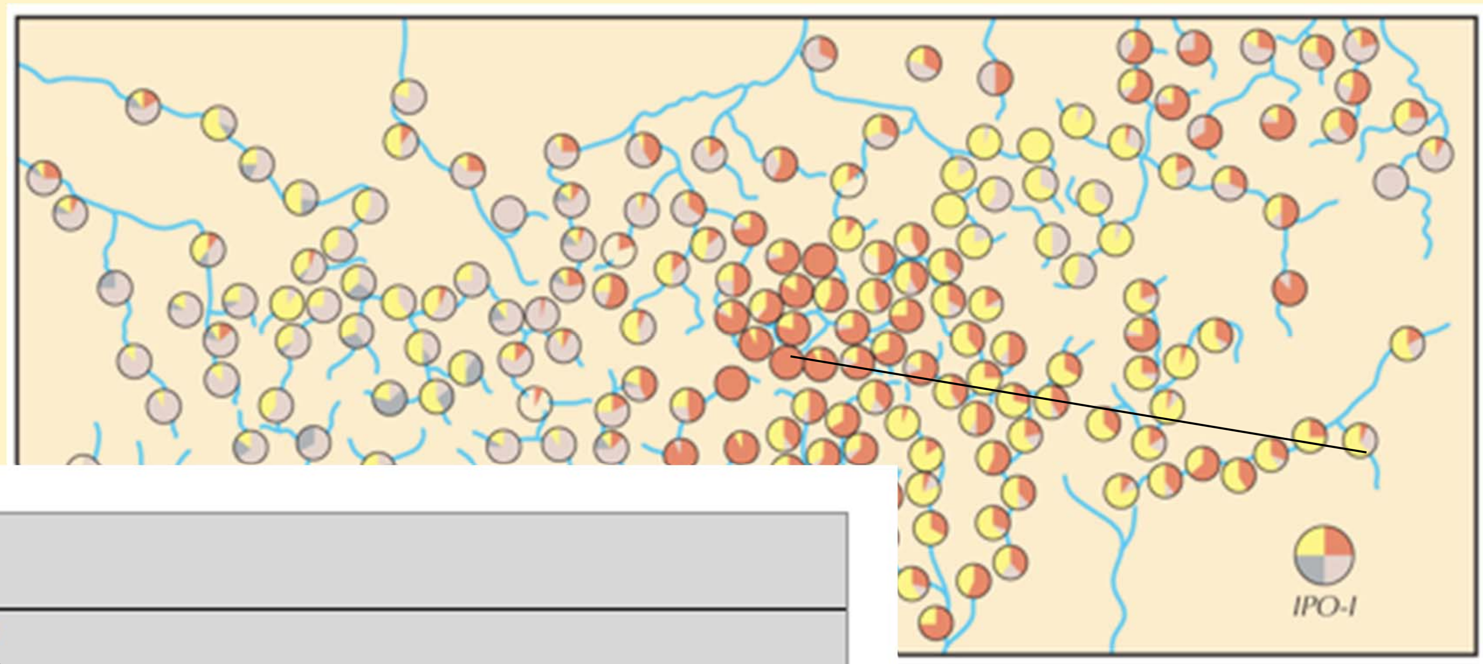
Space

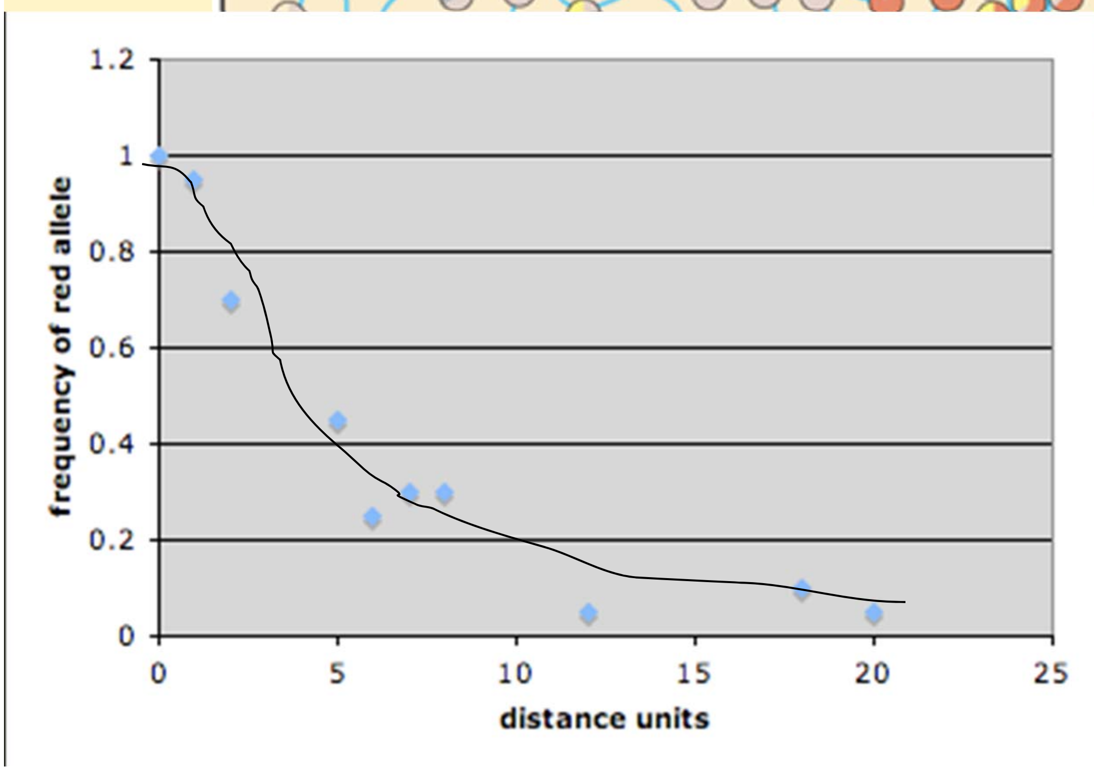
- Evolutionary and ecological processes are spatio-temporal (occur in time and space)
- So far we have only considered time

Variation in space



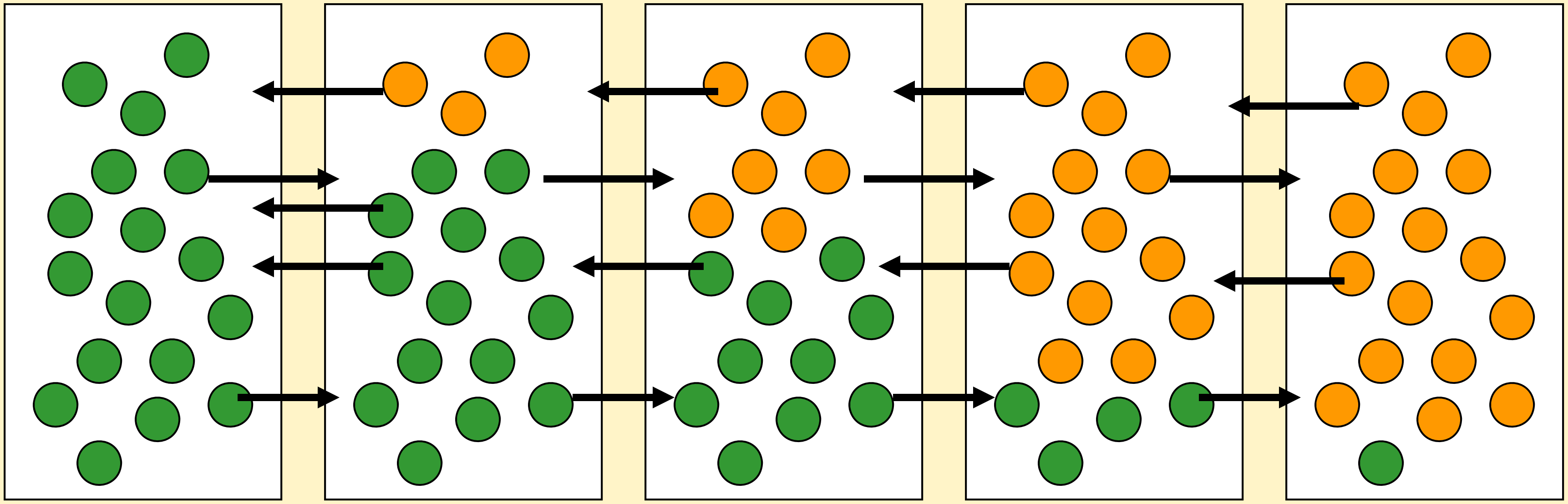
Geographic clines



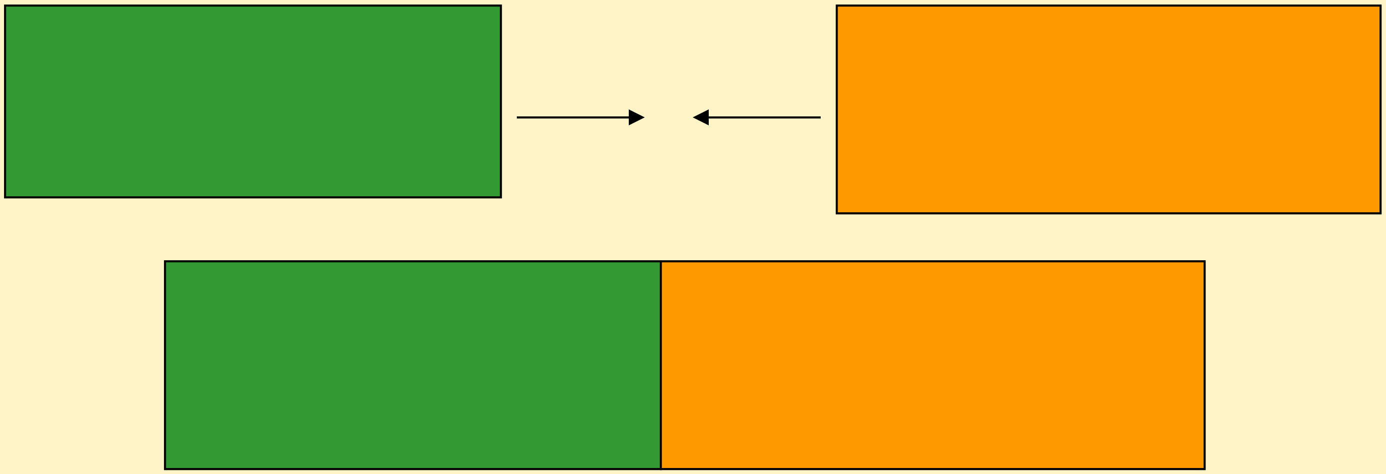


The cartoon version of a geographic cline

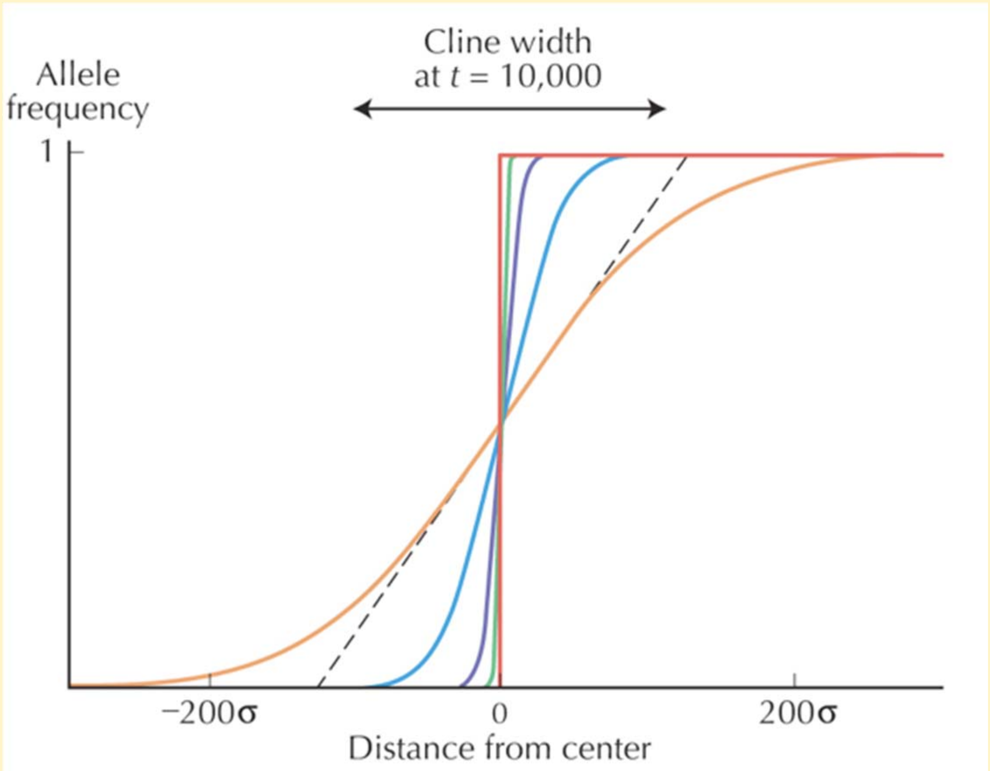
- Dispersal of alleles is much shorter than the width of the cline
- What will happen over time (if there are no other forces?)



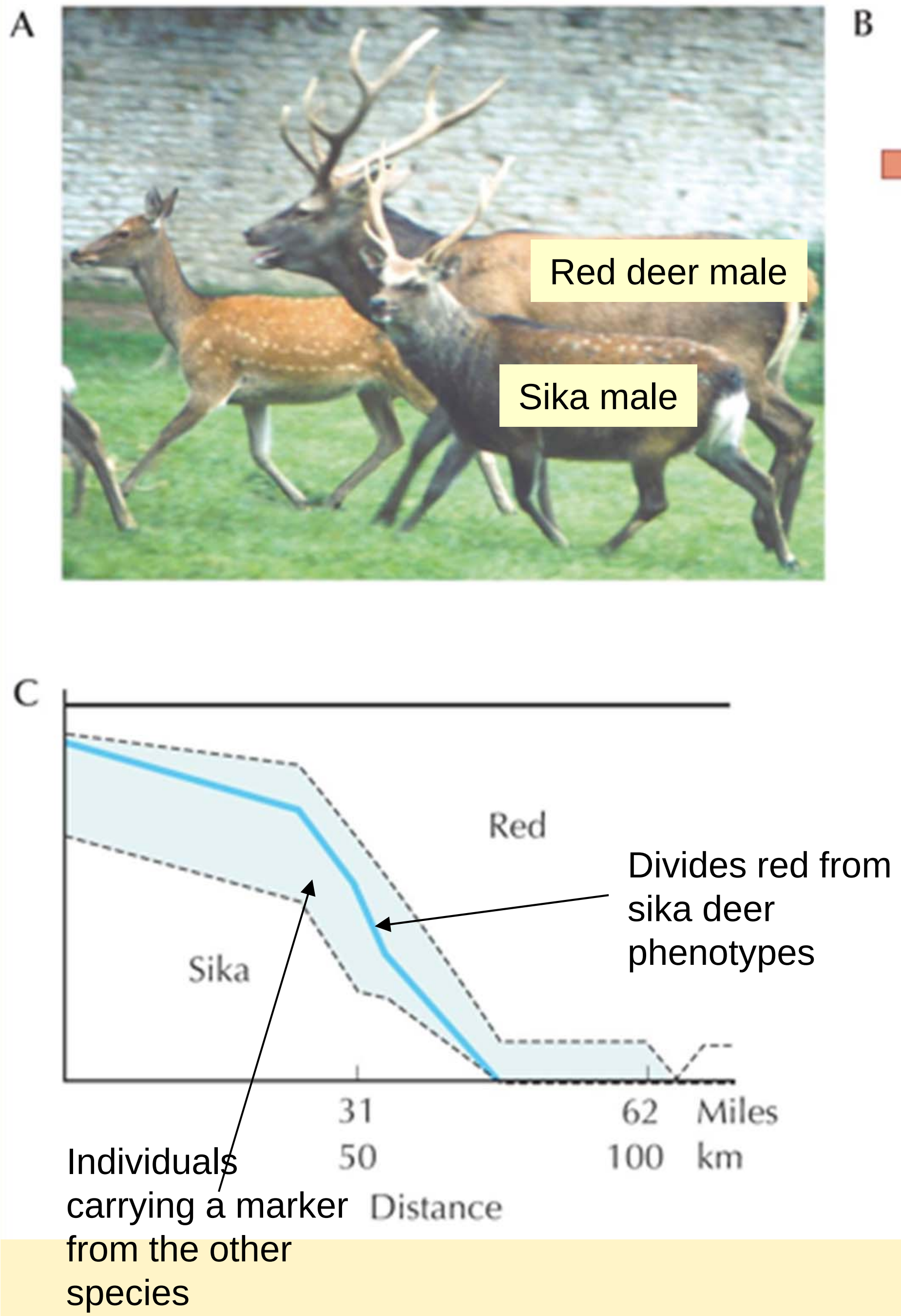
Evolution of clines



Frequency of “orange” allele over time



- Clines are built up by a diffusion process
- Clines get wider with time


A
Red deer male
Sika male
B
Red
Sika
Frequency
C
Red
Sika
Divides red from sika deer phenotypes
31
62
Miles
50
100
km
Distance
Individuals carrying a marker from the other species


Dundee
Oban
Perth
Stirling
Tarbert
Glasgow
EDINBURGH
Kintyre
Arran
Ayr
Jedburgh

Split of the population into two different ecotypes

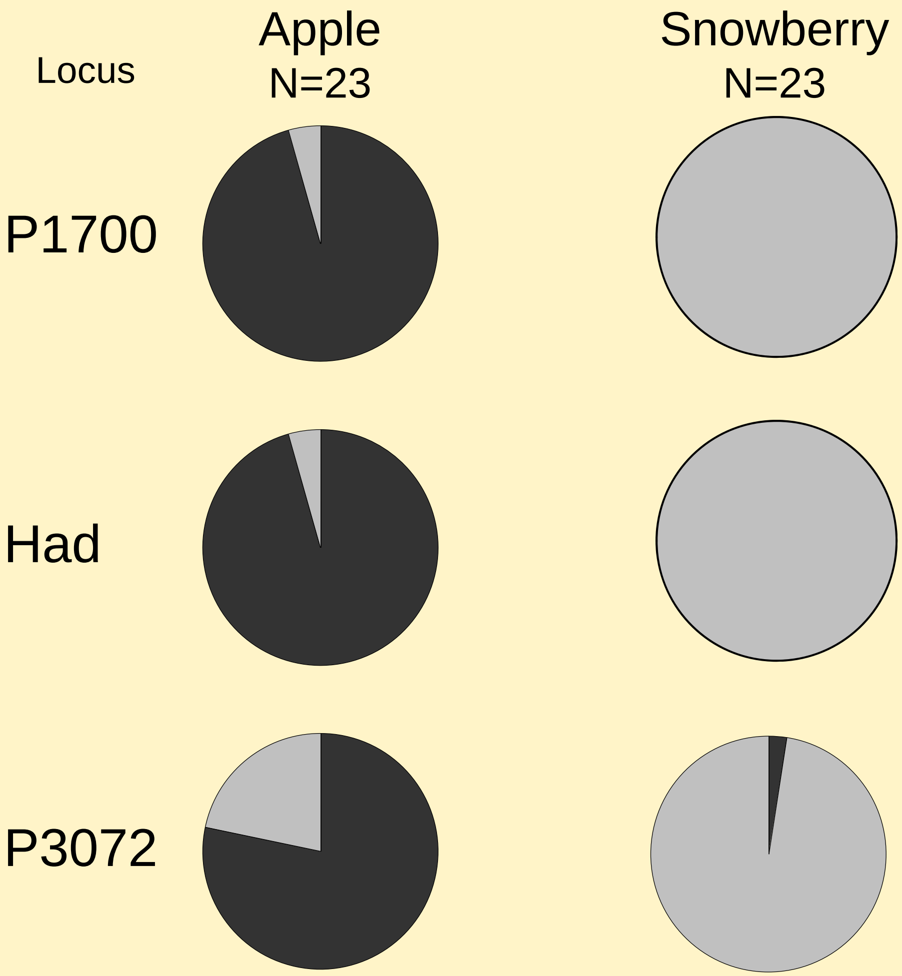
Apple maggots and snowberry maggots in Bellingham

Rhagoletis pomonella

Sibling species, morphologically identical

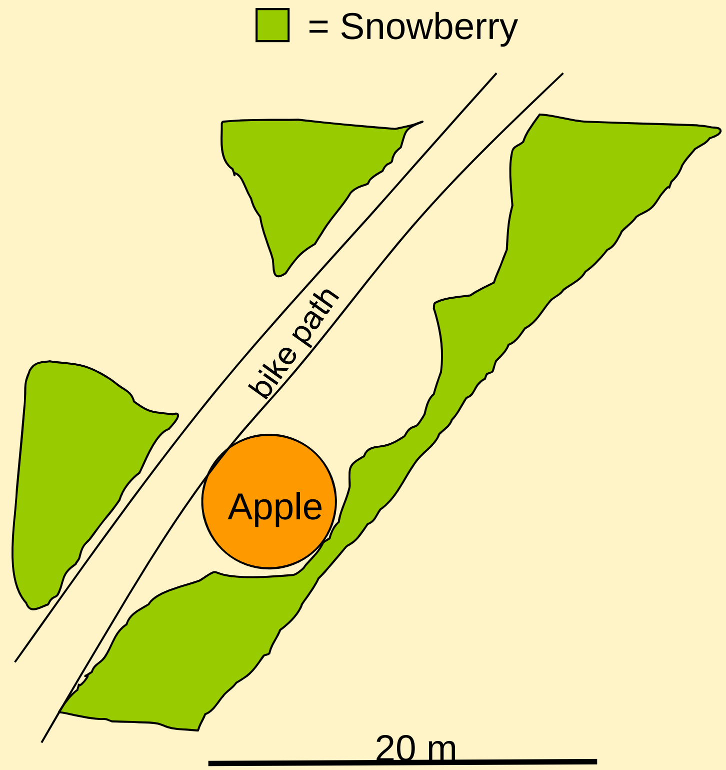
Rhagoletis zephyria

Why are they not mixing despite gene flow?



= "*pomonella* allele"
= "*zephyria* allele"

Allele frequencies at a micro-sympatric site along S. Bay trail, Bellingham, WA



The effect of selection on clines

- Alleles confer insecticide resistance in mosquitoes
- Coastal areas are sprayed in the summer